Effects of Hunting on a Puma Population in Colorado

Effects of Hunting on a Puma Population in Colorado

Kenneth A. Logan and Jonathan P. Runge

COVER PHOTOS

Top: Adult male puma (*Puma concolor*) M87, originally tagged as a 28-day-old cub on the Uncompahgre Plateau study area, Colorado, USA.

Bottom (left to right): Two adult females pumas associating with a male in background; Roubideau Canyon; four puma cubs in a nursery, Uncompahgre Plateau study area, Colorado, USA.

© CPW PHOTOS BY KEN LOGAN.

Table of Contents

List of Figures

14. Adult female puma annual survival rates associated with population trends in North America. Location designations refer to ID−UT1 and ID−UT2 (Idaho and Utah, Laundré et al. 2007), YBW and YDW (Greater Yellowstone Northern Range before and during occupation by wolves, respectively; Ruth et al. 2011, 2019), MT1 and MT2 (Montana, Robinson and Desimone 2011), WAL and WAH (Washington low and high harvest, respectively, Cooley et al. 2009*a*), COR and COT (this study reference period and treatment period, respectively), NM (New Mexico, Logan and Sweanor 2001), SD (South Dakota, Jansen 2011), PNW (Pacific Northwest, Lambert et al. 2006), UTL and UTH (Utah low and high harvest, respectively, Stoner et al. 2006).

List of Tables

ACKNOWLEDGMENTS

Allen E. Anderson was a researcher for the Colorado Division of Wildlife from the early 1960s until his retirement in 1991. He studied pumas on the Uncompahgre Plateau from 1981 to 1988. © PHOTO BY CLAIT E. BRAUN.

John M. Kane with adult male M1, the first puma we captured in this study, December 2004. © CPW PHOTO BY KEN LOGAN.

EXECUTIVE SUMMARY

We investigated effects of regulated hunting on a puma *(Puma concolor)* population on the Uncompahgre Plateau (UPSA; 2,996 km^2) in southwestern Colorado. We examined the hypothesis that an annual harvest rate averaging 15% of the estimated number of independent pumas using the study area would result in a stable or increasing abundance of independent pumas. We predicted hunting mortality would be compensated by: 1) a reduction in other causes of mortality, thus overall survival would stay the same or increase; 2) increased reproduction rates; or 3) increased recruitment of young pumas. Our alternate hypothesis was that an annual harvest rate averaging 15% of the estimated number of independent pumas would result in a declining abundance of independent pumas. Under this hypothesis, we predicted that hunting mortality would be additive, with: 1) no reduction in other causes of mortality, thus overall survival would decline; and neither 2) enhanced reproduction, or 3) enhanced recruitment would fully compensate for hunting mortality.

The study occurred over 10 years (2004−2014), and was designed with a reference period (years 1−5; i.e., RY1−RY5) without puma hunting and a treatment period (years 6−10; i.e., TY1−TY5) with puma hunting. We captured and marked pumas on the UPSA and monitored them year-round to examine puma demographics. We estimated abundance of independent pumas using the UPSA each winter during the Colorado puma hunting season from reference year 2 (RY2) to treatment year 5 (TY5) by using the Lincoln-Petersen method. In addition, we surveyed puma hunters to investigate how hunter behavior influenced harvest and the puma population.

We captured and marked 110 and 116 unique pumas in the reference and treatment periods, respectively, during 440 total capture events. Those pumas produced known-fate data for 75 adults, 75 subadults, and 118 cubs, which we used to estimate sex- and life stage-specific survival rates using program MARK. In the reference period, independent pumas using the UPSA more than doubled in abundance and exhibited high survival. Natural mortality was the major cause of death to independent pumas, followed by other human causes (e.g., vehicle strikes, depredation control). In the treatment period, hunters killed 35 independent pumas and captured and released 30 pumas on the UPSA. Abundance of independent pumas using the UPSA declined 35% after 4 years of hunting. Harvest rates of marked independent pumas with home ranges exclusively on the UPSA, overlapping the UPSA, and on adjacent management units representing the population-scale harvest averaged 22% annually in the same 4 years leading to the population decline. Adult females comprised 21% of the total harvest. Harvest rates from just the UPSA study area during the same period averaged 15%; but, as we note in the manuscript, the UPSA harvest estimate is biased and scale-dependent. The top-ranked adult survival model indicated a period effect interacting with sex best explained variation in survival. Annual adult male survival was higher in the reference period [$\hat{S}$ = 0.96, 95% Confidence Interval (CI) = 0.75−0.99] than in the treatment period ($\hat{S}$ = 0.40, 95% CI = 0.22−0.57). Annual adult female survival was 0.86 (95% CI = 0.72−0.94) in the reference period and 0.74 (95% CI = 0.63−0.82) in the treatment period. The top subadult survival model showed that female subadult survival was constant across the reference and treatment periods ($\hat{S}$ = 0.68, 95% CI = 0.43−0.84), while subadult male survival exhibited the same trend as adult male survival: higher in the reference period ($\hat{S}$ = 0.92, 95% CI = 0.57−0.99) and lower in the treatment period ($\hat{S}$ = 0.43, 95% CI = 0.25−0.60). Cub survival was best explained by fates of mothers when cubs were dependent ($\hat{S}_{mother\ alive}$ = 0.51, 95% CI = 0.35−0.66; $\hat{S}_{mother\ died}$ = 0.14, 95% CI = 0.03−0.34). The age distribution for independent pumas skewed younger in the treatment period. Adult males were most affected by harvest, with a 59% decline in their abundance after 3 hunting seasons, and no males >6 years old detected after 2 hunting seasons. Successful puma hunters used dogs, selected primarily males, and harvested pumas in 1−2 median number of days.

Pumas born on the UPSA that survived to subadult stage exhibited traits of both philopatry and dispersal. Local recruitment and immigration contributed to positive population growth in the reference period. But recruitment did not compensate for the losses of adult males and partially compensated for losses of adult females in the treatment period. Average birth intervals were similar in the reference and treatment periods (reference period = 18.3 mo., 95% CI = 15.5−21.1; treatment period = 19.4 mo., 95% CI = 16.2−22.6), while litter sizes (reference period = 2.8, 95% CI = 2.4−3.1; treatment period = 2.4, 95% CI = 2.0−2.8) and parturition rates (reference period = 0.63, 95% CI = 0.49−0.75; treatment period = 0.48, 95% CI = 0.37−0.59) declined slightly in the treatment period.

We found that a harvest rate at the population scale averaging 22% of the independent pumas over 4 years and with >20% adult females in the total harvest greatly reduced puma abundance. At this scale total human-caused mortality rate averaged 27% annually. Mortality rates of independent pumas from hunting averaged 6.3 times greater than from all other human causes and 4.6 times greater than from all natural causes during the population decline. Hunting deaths largely added to other causes of mortality, and reproduction and recruitment did not compensate for hunting mortality. Puma hunters exhibited selection for male pumas, reduced male survival, and affected the sex and age structure of the population. We discuss our results in relation to a synthesis of published information on pumas in North America. We recommend how regulated hunting in a source-sink structure can be used to conserve puma populations, provide sustainable puma hunting opportunity, and address puma-human conflicts.

Chapter 1. Introduction

Large carnivores in North America are managed and conserved depending upon peoples' values and institutional policies and actions (Young and Goldman 1946, Kellert et al. 1996, Pavlik 2000, Gill 2010, Clark et al. 2014). Species in this group include the jaguar (*Panthera onca*), wolf (*Canis lupus*), black bear (*Ursus americanus*), grizzly or brown bear (*U. arctos*), polar bear (*U. maritimus*), and puma (*Puma concolor*). These carnivores are hunted by humans for a variety of reasons: out of fear that the animals might attack them; to protect livestock and other wild animals deemed to have higher value; for subsistence or as commodities; for recreational gratification; and to obtain trophies for display (Amstrup et al. 1986, Pelton 2000, Clark et al. 2014). Unrestricted hunting of carnivores and state-sanctioned predator control programs up to the mid-1900s caused range-wide population declines and regional extirpations of the puma (Young and Goldman 1946, Cahalane 1964), jaguar (Brown and López González 2001), wolf (Young and Goldman 1944, Mech 1970, Brown 1984), black bear (Pelton 2000, Scheick and McCowan 2014), and grizzly bear (Mattson and Merrill 2002). As people recognized the rarity of these animals and society modernized, attitudes toward nature shifted from traditional domination and utilitarian views to more ecological, aesthetic, and compassionate ones that fostered tolerance and stewardship of large carnivores (Kellert and Berry 1987, Gill 2010, Teel and Manfredo 2009, Peek et al. 2012, Manfredo et al. 2018). These changes resulted in laws and policies to conserve sustainable populations of large carnivores while also managing them to satisfy the exigencies of people in changing environments.

In the United States, federal and state laws affected conservation of large carnivores. Large North American carnivores protected under the Endangered Species Act (ESA) have included the wolf, grizzly bear, jaguar, the Eastern cougar (*P. concolor couguar*) and Florida panther (*P. concolor coryi*; Department of the Interior 1973). Recent genomic taxonomy designates all pumas in North America as *P. concolor couguar* (Culver et al. 2000), therefore, the Eastern cougar was removed from the list in 2018 (U.S.

Fish and Wildlife Service 2018). Despite its lack of genetic subspecies status, the Florida panther has retained its ESA listing and is the only known breeding puma population in the eastern United States. Conservation activities under the ESA were effective in increasing the abundance and distribution of the Florida panther (Lotz 2017), wolf (Musiani and Paquet 2004) and grizzly bear (Schwartz and Gunther 2006, Kendall et al. 2009) in portions of their range in the United States. As populations of these carnivores meet established recovery goals and criteria for removal from the ESA list, management authority is granted back to the states encompassing the distribution of the species (e.g., the wolf in Montana, Montana Fish, Wildlife and Parks 2018). Likewise, state legislatures enacted laws conserving other large carnivores that were deemed more viable, including the puma in western North America and the black bear that identified these carnivores as harvestable species with game status and attendant restrictions on hunting. State wildlife management agencies were entrusted with enforcing the laws and developing management programs for these species at the behest of public beneficiaries and policy-makers (Pelton 2000, Anderson et al. 2010, Organ et al. 2012).

State management programs for carnivores enable wildlife managers to pursue a variety of objectives in the publics' interest, including carnivore conservation, hunting opportunity, human safety, reducing predation on wild ungulates and mitigating damage to private property, including livestock. Moreover, big game hunting opportunities generate revenue from the sale of hunting licenses and taxes on hunting equipment, which help finance law enforcement, habitat improvements, monitoring, and research. Together, public involvement, associated revenue, and professional management are key components of a process known as The North American Model of Wildlife Conservation (Organ et al. 2012).

Pumas gained the legal status of game animal in all of the western and Pacific states of the contiguous United States and the Canadian provinces of British Columbia and Alberta from 1965−1973. The states of North Dakota and South Dakota followed in 1991 and 2003,

respectively (Nowak 1976, Anderson et al. 2010). In California, the status of the puma was changed again to "specially protected mammal" in 1990, which prohibited recreational hunting of pumas (Updike 2005). In jurisdictions allowing hunting, state and provincial governments defined puma hunting seasons, and methods and amount of puma harvest. Restrictions on hunting apparently enabled puma populations to rebound from low numbers in the 1960s when, for example, 7 western states (California, Colorado, Idaho, New Mexico, Oregon, Utah, and Washington) each reported puma abundances in the hundreds (Cahalane 1964). By the early 2000s, those same states each reported puma abundances ranging from 2000−6000 (Becker et al. 2003, Whittaker 2005). As puma populations apparently increased, however, harvest also increased and may have contributed to populations stabilizing or declining in some western states, warranting attention from wildlife managers (Dawn 2002, Lambert et al. 2006, Nadeau 2008, Anderson et al. 2010, Montana Fish, Wildlife and Parks 2019).

In addition, the ecological role of pumas is integral to wildlife management and conservation. Pumas affect the abundances, distributions, and behavior of ungulate prey through predation (Hornocker 1970, Logan and Sweanor 2001, Laundré 2010) and compete with other carnivores (Kunkel et al. 1999, Ruth and Murphy 2010, Ruth et al. 2019). Remains of puma-killed animals also provision food for scavenging vertebrates and invertebrates (Elbroch and Wittmer 2012, Barry et al. 2018). These attributes, along with the puma's characteristically large home ranges and long-distance dispersal movements, identify it as a potential focal species for conservation planning (Beier 2010).

Public support for recreational hunting of pumas is diverse (Teel et al. 2002, Casey et al. 2005, Gigliotti 2005) and can restrict management options. Some public and legal challenges to hunting led to citizen ballot initiatives that prohibited puma hunting in California in 1990 and the use of dogs to hunt pumas in Oregon and Washington in 1994 and 1996, respectively (Mattson and Clark 2010, Negri and Quigley 2010). Consequently, in efforts to address

multiple interests, managers develop puma management objectives to ensure that populations hunted for recreation are sustainable, and to reduce puma abundance where needed to mitigate puma conflicts with people and predation on species of concern (Colorado Parks and Wildlife 2004). For managers to successfully attain such objectives, the effects of hunting on pumas must be understood. Thus, our research sought to inform management programs by examining the effects of hunting on a puma population in Colorado.

Theoretically, puma populations are naturally limited by available food and regulated by density-dependent competition (Pierce et al. 2000, Logan and Sweanor 2001, Laundré et al. 2007, Logan 2019, Ruth et al. 2019). Hunting mortality may perturb these natural processes. A puma population segment (i.e., adults and subadults) that is below its ecological carrying capacity (i.e., the natural limit of a population set by resources in the environment, Fryxell et al. 2014) and growing can sustain a certain level of hunting mortality without declining if hunting mortality is compensated (Williams et al. 2001). Compensation may result from reduced mortality rates from other factors (e.g., natural mortality), increased reproduction (e.g., larger litters, shorter birth intervals), or increased recruitment of young pumas born *in situ* or as immigrants. Any of these might occur if the removal of some animals through hunting improves conditions for surviving animals. If so, the puma population is expected to increase or remain stable despite hunting. If these mechanisms do not adequately compensate for hunting mortality, however, then hunting produces additive mortality to the extent that the puma population segment stops growing or declines over time. When this happens, hunting mortality limits population growth.

Information regarding the effects of hunting on puma populations was sparse prior to the initiation of our research. The first experimental removal of pumas occurred in Utah in 1987−1989 with a 1-time removal of 6 pumas (3 adults: 1 male and 2 female; 3 yearlings: 2 male and 1 female) in 1 winter (Feb−Mar), representing an estimated 27% of harvest-age (>1 yr. old) animals in the population, which included 6 dependent kittens (Lindzey et al.

1992). One year after removal, the abundance of adult pumas was almost fully recovered, except for possibly 1 male. The harvestable population, however, was still 27% below the pre-removal number because of a deficit of animals in the population >1 year old. The researchers also observed 2 other adult puma deaths in the same year which added to the total mortality. Thus, they concluded that a second year of similar removal could have furthermore delayed population recovery.

Researchers studying pumas in New Mexico from 1985−1995 used the rate of population growth independent of hunting to estimate harvest rates that might result in sustainable hunting mortality or declining populations (Logan and Sweanor 2001). The adult portions of 2 protected puma population segments were observed to increase by average annual rates as high as 17−28% over 3 four-year periods after initial declines were caused by culling pumas. The researchers found that puma population growth was apparently density dependent because average annual growth rates in adult puma abundance began to decline from 17% to 5% over 2 consecutive four-year periods. The average annual observed rate of increase was 11%. The authors suggested that sustainable hunting mortality of the puma population should not exceed 11% of the adult pumas per year. Conversely, if the objective was population reduction, hunting mortality in the puma population should exceed 11% of adult pumas per year.

Other sources in the literature did not produce useful information on puma harvest rates. An older reference that claimed a sustainable puma harvest up to 30% did not provide any data (Ashman et al. 1983). Another source used to support up to a 21% sustainable puma harvest rate came with a caveat from the original authors that "potential effects of this harvest rate were offset by [3] interceding years when no [pumas] were shot. It is unknown what annual harvest rate could be sustained and still allow for stability or growth in the population size" (Ross and Jalkotzy 1992:424).

Consequently, when Colorado Parks and Wildlife (CPW) managers developed state-wide puma hunting management plans in 2004 they had to rely on sparse information and their professional judgment (Colorado Parks and Wildlife 2004). To manage for a stable or increasing puma population, managers assumed that mortality rates of independent pumas [i.e., adults (usually >2 years old) and subadults (immature animals independent from mothers, usually 1−2 years old)] should fall in the range of 8−15% of an expected abundance of independent pumas. For a declining population, managers assumed that mortality rates should be ≥16% of the expected abundance of independent pumas (Apker 2005). Prior to our research, none of these puma hunting management assumptions had been tested for biological validity. To address this need, we examined effects of hunting on a puma population in Colorado. Our research was an un-replicated case study on 1 geographic area having a before and after treatment effect design without a separate control area where pumas were not hunted. Resources were not available for us to have implemented an equal study effort on a different geographic area as a control. Our study took place over 10 years (2004−2014) with 2 5-year periods: a reference period (years 1−5, hereafter RY1−RY5) and a treatment period (years 6−10, hereafter TY1−TY5). In the reference period puma hunting was prohibited; this provided baseline estimates for puma population variables without hunting. The treatment period occurred on the same study area and included regulated hunting to provide information on effects of hunting on the puma population.

To best assist CPW managers, we considered that the most important puma harvest assumption to investigate was the upper mortality limit expected to result in a stable or increasing population. Thus, our goal was to investigate harvest rates that maintained a stable or increasing abundance of independent pumas. Accordingly, we predicted hunting mortality would be compensated by: 1) a reduction in other causes of mortality, thus overall survival would stay the same or increase; 2) increased reproduction rates; or 3) increased recruitment of young pumas. Alternatively, we predicted that hunting mortality would be additive, and the population would decline. If mortality was additive, we expected to observe: 1) no reduction in other causes of mortality, thus overall survival would decline; and neither 2) enhanced reproduction, or 3) enhanced

recruitment would fully compensate for hunting mortality. In addition, we investigated whether the behavior of puma hunters influenced harvest structure and any emerging changes to the puma population sex and age structure. We did this by surveying hunters to gather information on their hunting methods and preferences.

Chapter 2. Study Area
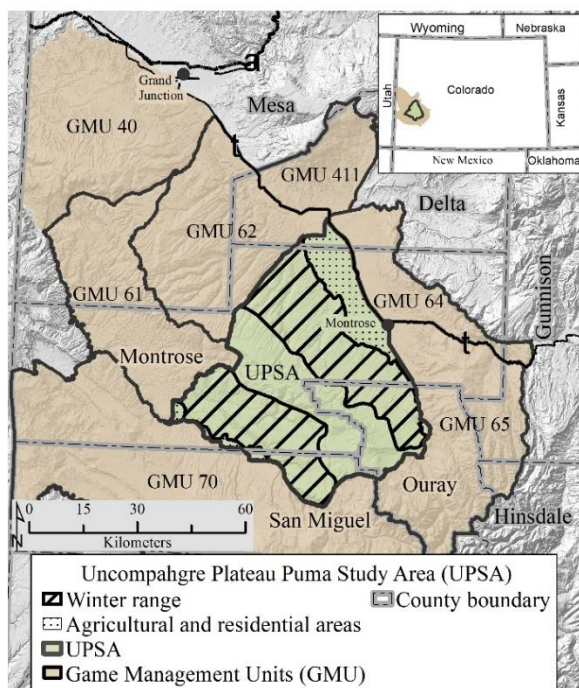
Figure 1. The Uncompahgre Plateau Study Area (UPSA) and surrounding Game Management Units (GMU) in Colorado, USA, 2004−2014.

The study area was the southern half of the Uncompahgre Plateau (in Mesa, Montrose, Ouray, and San Miguel Counties of Colorado, Fig. 1), a southeast-to-northwest oriented montane highland incised with canyons in the Colorado Plateaus Physiographic Province (Sinnock 1978). The Uncompahgre Plateau Study Area (hereafter UPSA) was 2,996 km^2 and was managed similarly to a Game Management Unit (GMU) except that puma hunting was manipulated for our research design. The UPSA would rank as the eighth largest by area of 185 GMUs in Colorado (range 71−4,460 km^2, average = 1,457 km^2). The UPSA included about 477 km^2 of agricultural and residential development on the east and west flanks, and about 2,519 km^2 of wild-land.

Vegetation on the UPSA transitioned from pinion-juniper (*Pinus edulis-Juniperus spp.*) covered foothills starting at about 1,700 m elevation to a Ponderosa pine (*Pinus ponderosa*) dominated woodland at mid-elevation, and up to the spruce-fir (*Picea engelmannii-Abies lasiocarpa, Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) forests at the highest elevations of about 3,000 m. Mid-elevation forests were interspersed with oak-serviceberry (*Quercus gambelii-Amelanchier alnifolia*) shrublands. Expansive sagebrush-steppe (*Artemesia spp.*-grass) meadows and basins occupied mid-to-high-elevations, especially in the south-central portion of the area.

Core winter range with pinion-juniper woodland along the San Miguel River on the southern edge of the Uncompahgre Plateau Study Area. © CPW PHOTO BY KEN LOGAN.

Weather was somewhat similar during the full reference period years 2005−2009 and treatment period years 2010−2014, as recorded at Sanborn Park on the west side of the UPSA (108°13′00″, 38°11′30″, 2,417 m elevation) by the United States Department of Agriculture, Forest Service (Western Regional Climate Center, 2005−2014 climate summaries, https://raws.dri.edu/wraws/coF.html. Accessed 2 Feb 2019). The reference period was characterized by an average annual precipitation of 35.5 cm (range 29.0−41.3), average December temperature of −4.6° C [range (−24.4)−13.3], and average July temperature 19.8° C (range 7.8−35.0). The treatment period was characterized by a slightly higher average annual precipitation of 45.8 cm (range 31.5−51.8), and similar average December

temperature −3.4º C [range (−23.3)−12.8] and average July temperature 19.4º C (range 2.2−33.9).

The prey community available to puma on the UPSA was diverse, and included both wild and domestic animals. Mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) abundances on the entire Uncompahgre Plateau based on modeled indices (White and Lubow 2002) in December each year of our study may have been 27,200−15,300, and 12,200−10,400, respectively, (Fig. 2, Colorado Parks and Wildlife, Terrestrial Section, unpublished data). Adult pumas on the UPSA preyed primarily on mule deer and elk, and killed them in approximately equal proportions (Alldredge et al. 2008). In winter (Nov−Mar) the study area provided a combined area of about 1,701 km^2 of lower elevation core winter range (980 km^2 east slope, 721 km^2 west slope) for pumas, mule

deer, and elk that migrated there as snow accumulated at higher elevations. Cattle (*Bos taurus*) and domestic sheep (*Ovis aries*) grazed on high-elevation summer ranges and low-elevation pastures in winter. Cattle were rare prey for pumas, with 1 recorded killed during this study. Sheep were occasional prey for pumas, with 10 recorded incidents during this study, each involving 1−20 sheep. Mostly rural, year-round human occupation occurred along the eastern, western, and southern fringes of the area. Other animals kept by people included alpacas (*Vicugna pacos*), llamas (*Lama glama*), goats (*Capra aegagrus domesticus*), and pigs (*Sus scrofa domesticus*). There were 5 recorded incidents of puma predation on these animals during this study, with each incident involving 1−4 animals (Unpublished records, Colorado Parks and Wildlife, Game Damage Program, Montrose, CO USA).
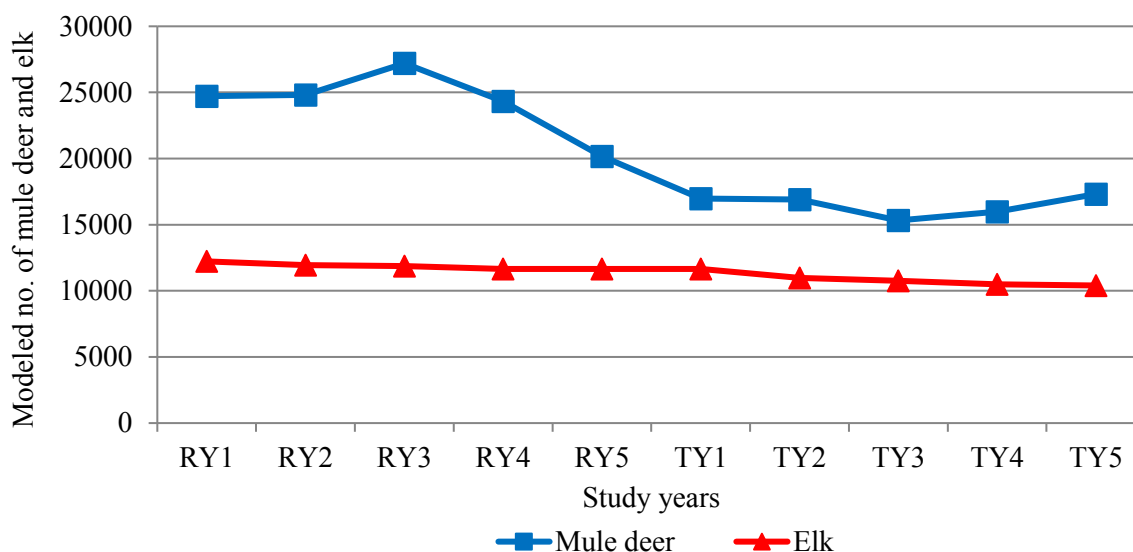
Figure 2. Abundances of mule deer and elk from modeled population indices during reference years 1 to 5 (RY1−RY5) and treatment years 1 to 5 (TY1−TY5), 2004−2014, on the Uncompahgre Plateau, Colorado, USA.

Potential competitors with pumas were coyotes (*Canis latrans*), black bears (*Ursus americanus*), and human hunters. Coyotes were subject to a year-round unlimited hunting season. Black bear hunting was regulated during a September to November season each year. Humans hunted mule deer and elk during annual fall big game seasons.

Prior to our research, pumas on the UPSA were subject to annual regulated hunting from mid-

November through March. During the 5 previous years (1999−2003) an average of 12 pumas (range 8−17) were reported killed by hunters on the study area each year (unpublished puma mortality records, Colorado Parks and Wildlife, Denver, CO USA). Based on the records of the sex and age classes of the pumas killed, 41% were classified as adult females; the rest were adult males and subadults of both sexes (Fig. 3). Two other puma deaths were

reported on the UPSA during that time-span; 1 adult male was shot by a landowner in 2002, and 1 subadult male was struck by a vehicle in 2003.
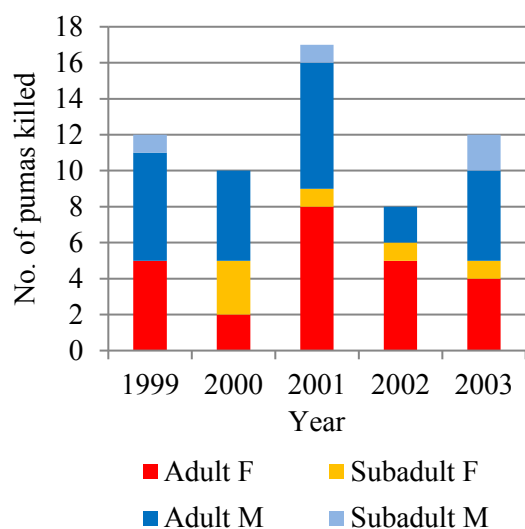
Figure 3. Number of pumas reported killed by hunters during 1999−2003 on the Uncompahgre Plateau, Colorado, USA.

Chapter 3. Methods

Puma research and management in Colorado

We designed this puma research within the existing context of puma management in Colorado. In Colorado, puma GMUs are subsets of 19 much larger Data Analysis Units (DAUs). Each DAU has a median of 6 (range 2−14) GMUs. DAUs range from 4,048−21,054 km^2 (average = 9,282 km^2) in size. GMU and DAU boundaries are delineated primarily so hunters can easily recognize boundaries (e.g., roads, rivers) for administering hunting management. We assumed GMUs and DAUs are not discrete puma populations because pumas are expected to move across administrative boundaries given that adult puma home ranges in North America vary in size from about 50 to 700 km^2 (Logan and Sweanor 2010) and puma habitat in Colorado is well connected (McRae et al. 2005). In addition, we expected dispersing subadults to move across GMU and DAU boundaries (Anderson et al. 1992, Sweanor et al. 2000).

CPW managers attempt to manipulate puma abundance with hunting at the DAU scale.

Within each DAU, they apply assumptions and judgments on puma density, sex and age structure, population growth rates, and impacts of hunting and other causes of mortality. The GMUs within DAUs are allocated a puma harvest quota (i.e., harvest limit) to spatially distribute harvest to achieve 1 of 2 desired DAU-wide puma population states: 1) a stable or increasing population to provide hunting opportunity and puma conservation, and 2) a declining or low phase population with hunting used to reduce puma conflicts with livestock, big game ungulates, and human safety. DAU management plans identify mortality rates of independent pumas expected to achieve the desired population states (i.e., 8−15%, ≥16%).

Puma hunting seasons began in mid-November and ended in March, at the latest. Quotas were not sex-specific. Successful hunters were required to report their puma kills to CPW within 48 hours of harvest and present puma carcasses for inspection within 5 days of harvest. Puma harvest within a GMU was updated daily, and hunters were required to call a free telephone number before each hunting day to check whether GMUs were closed because quotas had been reached. Puma hunting ended in each GMU when the quota was reached or the end of the hunting season, whichever came first.

Field methods

Puma capture, marking, sampling, and monitoring

Capturing, marking, and fitting individual pumas with telemetry collars and monitoring them was essential to a number of research objectives, including obtaining data on: population abundance, sex and age structure, reproduction, survival, mortality causes, and puma movements in relation to study area boundaries and emigration. We handled all pumas in accordance with approved CPW Animal Care and Use Committee (ACUC) capture and handling protocols (ACUC file #08-2004, ACUC protocol #03-2007) following the American Society of Mammalogists (Sikes et al. 2016). Captured pumas were marked with a telemetry collar, ear-tag (Allflex USA, Inc., DFW Airport, TX), and tattoo. An identification number tattooed in at least 1 pinna was permanent and could not be lost unless the pinna was detached.

Adult female puma F7 wearing eartags and a GPS collar which enabled us to gather data on the effects of hunting mortality on the puma population. © CPW PHOTO BY KEN LOGAN.

We captured pumas using trained dogs, cage traps, and by hand (for small cubs). Pumas captured with dogs usually climbed trees to take refuge. Adult and subadult pumas captured for the first time or requiring a change in telemetry collar were anaesthetized with Telazol (tiletamine hydrochloride/zolazepam hydrochloride) dosed at 5 mg/kg estimated body mass. The drug was delivered into the caudal thigh or shoulder muscles via a Pneu-Dart® shot from a CO_2-powered pistol (Pneu-Dart X-Caliber, Pneu-Dart Inc., Williamsburg, PA USA) or by a syringe at the end of an extendable pole. We deployed a 3m-by-3m square nylon net beneath the puma to catch it in case it fell. Pumas that fell into the net were immediately restrained with a catch-pole. If the puma stayed in the tree, one of us climbed the tree, fixed a rope to 2 legs of the puma and lowered the cat to the ground with an attached climbing rope. Some pumas jumped from the tree after being struck by the dart. In those cases we followed the puma's tracks until we found it sedated on the ground. To secure the puma, we covered its head, tethered it legs, and then monitored its vital signs. Normal signs were considered: pulse 70−80 bpm, respiration 20 bpm, capillary refill time ≤2 seconds, rectal temperature 38.3º C average, range 35−40º C (Kreeger et. al 1999). When a treed puma could not be safely immobilized and handled, we simply recorded the individual's sex, life-stage, association with other pumas (e.g., mother, siblings), and capture location prior to leaving it.

Capture teams usually consisted of 2 houndsmen and 2 biologists. In this photo, left to right: Jason Knight, Rick Navarette, Bruce Nay, James Waddell. © CPW PHOTO BY KEN LOGAN.

We used cage traps to capture adults, subadults, and large cubs (Bauer et al. 2005, Sweanor et al. 2008). We lured pumas to traps using road-killed or puma-killed ungulates. A cage trap was set only if a target puma (i.e., an unmarked puma, or a puma requiring a collar change) scavenged on the lure. We continuously monitored a set cage trap from about 0.5−1 km distance by using VHF beacons on the cage. This allowed us to respond to a captured puma in ≤30 minutes. We sedated pumas with Telazol injected into the caudal thigh or shoulder muscles with a syringe and restrained and monitored them as described previously.

We captured cubs at nurseries (i.e., nurslings) when mothers were away from the cubs as determined by radio-telemetry. Cubs ≤10 weeks old were captured using our hands covered with clean gloves or with a catch-pole. We did not sedate these cubs with drugs, and instead restrained them inside new burlap bags. We removed cubs from nurseries at distances of about 20–100 m to reduce our disturbance of the nurseries. We returned the cubs to the exact nurseries immediately after completing the sampling process (Logan and Sweanor 2001).

Captured adult and subadult pumas were fitted with Global Positioning System (GPS) or Very High Frequency (VHF) collars, each weighing about 400 g (Lotek GPS 4400S) and 300 g (Lotek LMRT-3, Lotek Wireless, Newmarket, Ontario, Canada), respectively. Budget constraints limited the number of GPS collars available annually; therefore, GPS collars were

fitted primarily to adult pumas of both sexes. Other adult and subadult pumas were fitted with VHF collars.

We attempted to collar all cubs in each observed litter of nurslings with a small VHF transmitter (model 080, Telonics Inc., Mesa, AZ USA) mounted on an expandable collar, total weight 62 g, when cubs weighed 1.3−10 kg. The collars could expand to 54 cm circumference to accommodate growth to the adult stage. Cubs weighing ≥7 kg were fitted with a larger expandable collar weighing 90 g (model 210, Telonics Inc., Mesa, AZ USA), that also could expand to 54 cm circumference. Cubs approaching the age of independence (11−14 months old) were fitted with Lotek LMRT-3 VHF collars each with a leather expansion link that added 10−14 cm to the collar circumference to accommodate the adult puma neck size.

Adult male puma captured in a cage trap and about to be anesthetized by biologists Robert Alonso (left) and Brady Dunne (right). © CPW PHOTO BY KEN LOGAN.

Volunteer biologist Linda Sweanor with 5-week-old female cub F189 wearing an expandable collar that enabled us to quantify data on cub survival and agent-specific mortality. © CPW PHOTO BY KEN LOGAN.

We initially estimated the ages of adult pumas by the gum-line recession method (Laundre et al. 2000) and later with dental characteristics of known-age pumas (i.e., observed from cubs to older ages) from this study. We recognize these aging methods are not exact for pumas with unknown histories. We found them useful, however, to place individual pumas into 2-year age increments to examine age structures and to back-age certain adult pumas into previous winter counts assuming we missed detecting them on the UPSA until they were about 2+ years old (see **Analysis**, *Puma abundance and growth rates* and *Puma sex and age structure*). Ages of subadult and cub pumas were estimated initially based on dental and physical characteristics of known-age pumas from New Mexico (Logan and Sweanor unpubl. data) and later from known-age pumas in this study. We estimated the ages of nurslings from birth dates indicated by GPS- and VHF- location data of collared mothers.

We focused our capture efforts of independent pumas (i.e., adults and subadults) in winter to gather data on harvest-age pumas in association with the Colorado puma hunting season. During the reference period when no hunting was allowed, our capture team operated from early snow accumulation in November until April when high ambient temperatures and black bear emergence from hibernation impacted the dogs' effectiveness. During the treatment period we began our dog-assisted capture operations after the UPSA puma-hunting quota was reached (Dec−Jan) so as not to interfere with hunters' activities or harvest preferences. Although this could have resulted in a shorter dog-assisted capture period, it was mitigated by deploying 2 capture teams. Houndsmen in our capture teams were not allowed to hunt pumas for sport on the UPSA during the treatment period.

The UPSA was accessible by roads and trails, enabling us to canvass the study area repeatedly each winter, and thereby facilitated our detection and capture of pumas. We searched less accessible areas by hiking canyon rims and bottoms to detect puma tracks while allowing dogs to freely search for the animal's scent. Our objective was to apply intensive, uniform searching effort and to directly monitor via radio-telemetry a large majority of independent pumas that used the UPSA each winter. Thus, we prioritized our efforts to detecting and capturing non-collared independent pumas. When we followed fresh puma tracks that led us to <1 km (usually <0.5 km) from GPS- and VHF-collared individuals based on strengthening radio signals, we re-directed our efforts away from those pumas and toward finding non-collared ones.

We monitored radio-collared pumas year-round. GPS collars were programmed to fix locations 4 times per day (0600, 1200, 1900, 2400) during RY1−TY2, then 2 times per day (1200, 2400) during TY3−TY5 to extend battery life. We attempted to locate all collared pumas once per week from fixed-wing aircraft as weather and scheduling conditions allowed, and opportunistically from the ground (Logan and Sweanor 2001). We checked the live or dead signal status from collared pumas during aerial and ground telemetry. VHF and GPS collars had mortality modes set to alert researchers when

animals were immobile for 3 hours and 24 hours, respectively, so that dead ones could be examined. We downloaded GPS collars remotely roughly once per month to retrieve location data. Emigration from the study area was revealed by movements of radio-collared animals or hunter returns of ear-tags from pumas killed outside of the study area. We investigated female pumas for evidence of reproduction whenever they exhibited constrained movements over a 1−4 week period with GPS and VHF location clusters of <300 m radius or recurrent movements to farther distances that returned to focal locations (Logan and Sweanor 2001).

Puma hunting manipulation

In the 5-year reference period, puma hunting was prohibited on the UPSA. In addition, any radio-collared or ear-tagged pumas that ranged off the UPSA onto GMUs 61 and 62 north of the UPSA were protected from hunting (Fig. 1). Otherwise, pumas that were involved in depredation on livestock and public safety events on the UPSA and elsewhere could be killed following established CPW management policies.

In the 5-year treatment period, pumas on the UPSA were subjected to regulated hunting. The puma hunting season began in mid-November and ended the date that the last puma on the quota was killed each winter. The initial harvest quota was set at 8 pumas which represented a 15% target harvest of the estimated number of 53 independent pumas using the UPSA in TY1. This estimate was modeled from puma count data in winter RY4. After we detected a linear decline in winter counts of independent pumas during TY1−TY3, we used a simple linear regression model to project the expected count for independent pumas for TY4. The model projected 44 pumas, so we adjusted the harvest quota down to 5 pumas, an expected 11% target harvest in TY4, to examine the effect of a reduced harvest on puma abundance. The quota of 5 also was applied in TY5 (see **Analysis**, *Puma abundance and growth rates* below, and **Appendices I** and **II**).

During our 10-year study, puma hunting quotas on the GMUs bordering the UPSA did not vary annually, except in GMU 65. There annual quotas were 5 in RY1−RY4, 4 in RY5 and TY1,

5 in TY2 and TY3, and 6 in TY4 and TY5. All GMUs bordering the UPSA were in 2 DAUs of which 1 (including GMUs 61, 62, 64, and 65) had a management objective for a stable puma population and 1 (with GMU 70) had a management objective for a stable or increasing population (Fig. 1).

Puma hunter information
Puma hunters on the UPSA were required to adhere to the same regulations as others in Colorado. Consistent with Colorado's puma hunting management, the number of hunters on the study area each winter was potentially unlimited, because the actual puma harvest was limited by the quota. Puma hunters on the UPSA, however, were mandated to obtain a special hunting permit. Each hunter could obtain the free hunting permit from the CPW Service Center in Montrose, CO, USA. Each permit allowed the individual hunter to hunt in the UPSA for 14 days from the issue date. Unsuccessful hunters that wanted to continue hunting past the permit expiration date could get serial 14-day permits until they harvested a puma, stopped hunting, or until the end of the hunting season. Each hunter also received a voluntary survey with their puma hunting permit and a stamped return envelope. Hunters were asked to complete the survey as soon as possible for each hunting period associated with the permit. Responsive hunters either mailed-, or handed-in their surveys. If hunters did not respond to our first request, we tried to contact them a second time by telephone or in person, and asked them to complete and return the survey.

The permit system and survey responses provided data on hunters that included: 1) permit holders that actually hunted on the UPSA; 2) number of days each hunter hunted on the UPSA; 3) the sex of puma that made the first set of tracks <1 day old that a hunter encountered on the UPSA (representing the first theoretically "catchable" puma encountered; we provided hunters with the same measurements we used to distinguish male and female tracks, see **Analysis**, *Puma abundance and growth rates*); 4) the sex and life-stage of a puma harvested by the hunter on the UPSA; 5) counts and sexes of independent pumas that were captured and released by hunters on the UPSA; 6) if marks on

the pumas (i.e., collar, ear-tags) influenced a hunter's decision to harvest an animal; 7) if the hunter hunted with dogs; and 8) hunter self-identification as a selective or non-selective hunter. On this last point we provided hunters these definitions: A selective hunter is one that purposely is hunting for a specific type of legal puma, such as a male, large male, or large female. The selective hunter attempts to distinguish between male and female tracks, and large and small males or females before taking the animal. This type of hunter is willing to pass up pumas that are detected from tracks or when treed. A non-selective hunter is one that intends to take whatever legal puma is first encountered or caught, with no preference for sex or size.

Each puma harvested on the UPSA was visually examined by our research personnel and officially marked with a metal, numbered tag to indicate legal possession by the hunter, consistent with Colorado puma hunting regulations. At the time of carcass check-in, a CPW mandatory harvest form also was completed, which included the puma's sex, age estimate, date of kill, and kill site location.

The head and skin of harvested male puma M165 after it was inspected by biologists and tagged to indicate legal possession by the hunter. © CPW PHOTO BY KEN LOGAN.

Analysis

Response variables
We estimated responses of the puma population to hunting and other mortality factors based on 5 population processes: 1) abundance of independent pumas, 2) cause-specific mortality rates, 3) survival rates, 4) reproduction rates, and

5) sex and age structure of the independent pumas in the population.

Puma abundance and growth rates
The parameter of interest to wildlife managers was the abundance of independent pumas (i.e., adults and subadults) November through March each winter coinciding with the puma hunting season in Colorado. Initially, we obtained an index to abundance of independent pumas that used the UPSA based on counts of pumas we detected from November through March (i.e., winter counts) from RY4−TY3 (**Appendix II**). We used this information for setting the hunting quotas in the treatment period. Winter puma counts consisted of the sum total of all known marked pumas, non-marked pumas we captured but could not safely handle, and non-marked pumas harvested on the UPSA. In addition, our counts included other pumas of unknown identity detected by their tracks as recorded by our capture teams on the study area if their track characteristics fit these criteria: 1) did not match known movements and locations of radio-collared pumas, 2) exhibited diagnostic measurements of unique individuals [i.e., tracks distinguishing sex from hind-foot plantar pad inside width measurements ≥52 mm classified as male, ≤50 mm classified as female; ≥2 mm difference in hind-foot plantar pad widths (measured with a steel ruler)], and 3) different counts of cub tracks with mothers' tracks.

After all our data on puma winter capture efforts, observed mortalities, and fates of pumas with non-functional collars were compiled, we used the Chapman method for the Lincoln−Petersen (LP) estimate (Petersen 1896, Lincoln 1930, Pollock et al. 1990) to estimate the number of independent pumas (i.e., $\hat{N}_c$) that used the UPSA from November through March each winter from RY2–TY5.
$\hat{N}_c = [(n_1 + 1)(n_2 + 1)/(m_2 + 1)] - 1$ (Pollock et al. 1990, equation 2.2).
This approach also provided estimates of variance
var $\hat{N}_c = (n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)/(m_2 + 1)^2(m_2 + 2)$ (Pollock et al. 1990, equation 2.3) and precision with 95% CIs
$\hat{N}_c \pm 1.96 (\text{var } \hat{N}_c)^{0.5}$ (Pollock et al. 1990:11).

We treated each entire capture and hunting season (Nov−Mar) as a single sampling period.

This extended capture effort potentially minimized bias from capture heterogeneity by allowing sufficient time for us to search the entire study area, to use data on puma captures both from our study team and hunters, and to detect individual pumas with home ranges that overlapped both inside and outside of the UPSA. We defined the LP parameters as: n_1 = the number of marked independent pumas we expected to be using the UPSA at the start of each November, n_2 = the total number of independent pumas detected during the hunting and capture season, and m_2 = the number of the n_2 sample that was previously marked. $\hat{N}_c$ was then an estimate of the number of independent pumas that used the UPSA during the November−March period and before any pumas were removed from the population. Detections consisted of marked independent pumas recaptured by hunters, previously marked pumas we recaptured during our winter capture operations, and radio-collared pumas we detected by following tracks toward radio signals of pumas during our ground capture operations. Radio-collared adults in the n_1 data with home ranges that overlapped the UPSA and adjacent areas were counted as detected in the m_2 data if they were harvested on a portion of their home range off the UPSA. Adult pumas with failed radiocollars that had previously established home ranges on the UPSA were counted in n_1 data in winters they were not detected if they were subsequently either recaptured or harvested (i.e., their fates were known) on the UPSA in subsequent winters. In addition, we back-aged pumas with estimated ages ≥3 years old that we caught for the first time and assumed they were present on the UPSA the previous winter(s) up to when they were 2+ years old (e.g., a puma aged 3.5 years old in TY2 would be counted as a 2.5 year old in TY1, Logan and Sweanor 2001); those pumas were counted in the n_2 data. We used the change in the LP $\hat{N}_c$ estimates of independent pumas and the 95% CIs as one gauge of changes in the abundance of independent pumas that used the UPSA during the reference and treatment periods. We recognize that this estimate of abundance assumes the population is closed, which this population is not. Therefore the abundance estimates are biased (Seber 1982). However, this method is an improvement on the use of simple counts that are more susceptible to

biases due to annual changes in detection probability and also more prone to errors of underestimation.

We also estimated the finite rate of increase (λ) and its 95% CI each year during the reference and treatment periods, RY2–TY5, to interpret changes in abundance of independent pumas without and with the hunting treatment (Fryxell et al. 2014). To calculate λ and 95% CIs, we drew 10,000 samples using R statistical software (version 3.1.1 R Core Development Team, 2014) for each year from a normal distribution using that year's LP $\hat{N}_c$ estimate and its standard error. We calculated λ for each set of 10,000 samples by dividing the resulting estimate one year forward by the current year. The estimated λ was the median of this sample and the 2.5th and 97.5th percentile values defined the bounds of the 95% CI. The estimate of λ would be prone to bias, like the LP estimate, if immigration and emigration rates changed annually.

Puma sex and age structure

We quantified the sex and age structure of independent pumas on the UPSA each winter RY1–TY5 based on the LP estimates of adult and subadult pumas. We also used counts of cubs we captured and counts of non-captured cubs we detected from tracks associated with mothers. We graphically analyzed the sex and age structure of independent pumas that we physically examined (i.e., pumas captured and handled or harvested). Independent pumas were placed in 2-year age increments (i.e., 1–2, >2–3 yr, and so on). The sex and age structures during the reference period (i.e., RY1–RY5) and up to the start of TY1 represented the population protected from hunting but subject to other causes of mortality and just before any pumas were removed in TY1. The subsequent age structures for the remainder of the treatment period (i.e., TY2–TY5) represented when hunting and other mortality factors affected the independent pumas.

Puma mortality

We estimated cause-specific mortality rates of independent pumas on 2 spatial scales. The smaller, local scale included the number of independent pumas estimated to use the UPSA each winter, consistent with the way managers might conceive of applying harvest limits (i.e., quotas) to GMUs. The larger scale included the UPSA and 4 GMUs bordering the UPSA where marked pumas ranged (i.e., GMUs 61, 62, 65, 70; total area = 11,614 km^2; none were on GMU 64). We examined fates of independent pumas at this larger scale for 2 reasons: First, managers considered puma population segments at a DAU-scale for setting broad population state objectives. Thus, we use the term "population-scale" in referring to parameters associated with this larger scale. Second, we recognized that the local UPSA puma population was open and could be affected by fates of pumas ranging on the UPSA and adjacent GMUs (i.e., pumas with home ranges overlapping the UPSA and prospective immigrants to the UPSA could be killed by hunters on adjacent GMUs).

The smaller scale represented puma mortality rates on the estimated number of independent pumas that used the UPSA each hunting season. We examined these mortality rates by using 2 metrics. The first metric represented the proportion of the expected number of independent pumas using a GMU that died within the boundaries of the GMU. We used simple quotients with the numerator as the number of independent pumas observed to have died within the UPSA boundaries each hunting season and the denominator being the LP $\hat{N}_c$ estimated number of independent pumas using the UPSA each hunting season. We note that these estimates were biased because the use of LP estimates in an open population is itself biased (Seber 1982). Furthermore, the numerator only included animals harvested within the UPSA boundaries, but the denominator included animals ranging on and off the UPSA; thus, the estimate was biased low. We include these estimates here to represent how managers may view harvest rates on management units that are small relative to the population. In the second metric we accounted for the radio-collared pumas with home ranges overlapping the UPSA that were counted in the denominator and died on adjacent GMUs because their deaths affected future abundance estimates on the UPSA (i.e., independent pumas that died within the UPSA boundaries + marked independent pumas with

overlapping home ranges that died on adjacent GMUs / LP $\hat{N}_c$ estimate of independent pumas using the UPSA). This metric could partially mitigate the biases in the first metric, but could not account for any non-marked pumas with home ranges overlapping the UPSA and estimated in the denominator that might have died on adjacent GMUs.

At the "population-scale", we used all the marked independent pumas with known fates that ranged on the UPSA and on the 4 GMUs bordering the UPSA where marked pumas were reported to have died to calculate annual rates of agent-specific mortality. We used simple quotients with the numerators being the number of marked individuals that died each biological year (i.e., Nov−Oct, see *Puma survival* below) and the denominators being the number of marked independent pumas alive at the beginning of each biological year. Likewise, we calculated rates at which marked pumas emigrated beyond the boundaries of the GMUs bordering the UPSA and considered those to be extra-population-scale movements. We calculated 95% simultaneous CIs for the resulting multinomial proportions (Goodman 1965, May and Johnson 1997) of cause-specific mortality and movement.

For cubs, we counted mortalities and categorized them by proximate cause of death. We report numbers and percentages for each mortality type for the reference and treatment periods. We analyzed if there was a difference in the proportions of litters subject to infanticide in the reference and treatment periods by calculating the binomial proportions and Clopper-Pearson exact 95% CIs by using the PROC FREQ procedure in SAS (Version 9.3, 2010, SAS Institute).

Puma philopatry, dispersal, and emigration

Pumas born on the study area were defined as philopatric if their cumulative adult home range locations overlapped their mothers' cumulative home range locations. Pumas born on the study area were considered to have dispersed if no portion of their adult home range locations overlapped their mothers'. Dispersal distances were measured in kilometers using the planar measuring tool in ESRI, Arcmap 10.2 from first captures at nurseries, with mothers or siblings,

or as independent pumas to dispersal end points of last radio-telemetry locations or their mortality sites (e.g., harvest, vehicle strike, depredation control). We estimated ages at independence (i.e., separation from mothers) and dispersal of previously radio-collared cubs, and reported medians, averages, and 95% CIs. Pumas that moved completely outside the boundaries of the UPSA were considered emigrants. Those included some young independent pumas that were captured and marked on the UPSA that could not be connected with known mothers, but subsequently exited the UPSA. We estimated a minimum frequency of emigration of offspring from the UPSA by using the known fate data on the radio-collared cubs we used in the survival analysis (below). Notably, these emigration rates were expected to be higher than the extra-DAU-scale emigration rates we estimate in *Puma mortality*, because of the shorter movement distance needed for pumas to exit the UPSA.

Puma survival

We investigated puma survival in the reference and treatment periods to assess any effects of hunting. We defined the biological year for adult pumas as the period from November (the month that puma hunting seasons began) through the next October to encompass complete hunting seasons. Survival rates of subadults and cubs were estimated for 12-month periods representing those life stages. We used the known-fate data type and logit link function in program MARK (White and Burnham 1999) (accessed 12 Jan 2015) to model survival rates with a candidate set of models that might explain variation in survival (see *Covariate selection, model selection, and inferences*, below).

Adult pumas were defined as >2 years old, unless we had evidence that they bred at an earlier age. In western North America, average ages of first breeding for samples of known-age females ranged from 23−28 months old and averaged 26.1 months (Utah *n* = 6, Lindzey et al. 1994; New Mexico *n* = 12, Logan and Sweanor 2001; Alberta *n* = 6, Ross and Jalkotzy 1992; Montana *n* = 14, Robinson and DeSimone 2011). That average was close to the estimated average age of 29 months of first conception for a sample of 14 females in this study (see **Puma**

reproduction in **Chapter 4. Results**). Furthermore, because our capture efforts for independent pumas were focused during November to April, the youngest pumas in the adult stage in November generally could have been 26−32 months old, assuming the pumas were born within the monthly distribution of puma births in our study. We did not have data on first reproduction for males in our study; however, males in New Mexico were estimated to reach sexual maturity at about 2 years old (Logan and Sweanor 2001).

Adult puma survival and mortality were examined from data on radio-collared pumas. Radio-location records for each adult puma were converted to monthly encounter histories. We used program MARK to estimate monthly survival rates while allowing staggered entry based on when we collared individuals and censoring of individuals if we lost contact with them (Pollock et al. 1989). We used data from RY2−TY5. We did not use data from RY1 because we had collared only 7 adult pumas (3 males and 4 females). Encounter histories of individual adult pumas started on the day of capture or the beginning of RY2 (i.e., 1 Nov 2005) for surviving pumas that were captured previous to that date. We censored individuals if we did not receive their radio-telemetry signal after the month of their last location. Individuals re-entered the data set if we recaptured them and fit them with a new collar. Death dates were known for individuals killed and reported by hunters, individuals killed for depredation control, and for some vehicle strikes. For pumas that died of other causes, death dates were assigned to pumas with GPS collars based on the first day that GPS locations indicated that the pumas were immobile. For VHF-collared pumas, dates were estimated as the mid-point of the span of days in which the puma was estimated to have died based on detection of radio-collar mortality signals and carcass decomposition. Causes of death were categorized as human causes (e.g., hunting, depredation control, vehicle strike, illegally killed), known natural causes (e.g., intraspecific killing), or unknown natural causes (e.g., presumed disease-related).

Subadult pumas are independent of their mothers and usually do not participate in breeding behavior (Logan and Sweanor 2001). Subadult puma survival and mortality was estimated for all known radio-collared, ear-tagged, and tattooed pumas with known fates. Individual pumas entered the subadult stage under two conditions: 1) after they were known to be independent from their mother based on radiotelemetry, or 2) at 13 months if their date of independence was not known. We used 24 months for the upper end of the range for subadults and 13 months as the lower end. Thirteen months is the median age (average = 13.7 months) for a sample of 15 pumas at known age of independence in this study (see **Puma philopatry, dispersal, and emigration** in **Chapter 4. Results**). Because we did not know exactly when all of the pumas in this life stage became independent, some of the pumas may have been dependent cubs for ≥13 months. Encounter histories for the pumas started when marked pumas entered the life stage and on the first day of capture for subadults caught and marked for the first time. Individual radiotelemetry records were converted to monthly encounter histories. Death dates were assigned to reported harvest, depredation control, and vehicle strike dates. If mortality dates for VHF-collared individuals were not observed, we examined the individual's radiotelemetry data and state of decomposition of the carcass and used the mid-point of the span of days in which the puma was estimated to have died.

Cub survival and mortality were estimated for radio-collared pumas between 1−12 months old. Because the youngest cubs we radio-collared were 25 days old, we could not estimate mortality and survival rates for younger cubs. The large majority (i.e., 85 of 118) of cubs in this data set were initially radio-collared as 1−2 months-old nurslings. We entered older cubs we collared in the analysis because we converted individual radiotelemetry records to monthly survival histories based on age. This simply allowed us to increase the sample sizes of cubs we monitored in the older months. Encounter histories for the cubs started on the first day they were collared. We assigned a cause of death to each cub mortality and recorded known dates of death. If dates of death were not observed, however, we used the mid-point of the span of days in which the puma was estimated to have

died based on the radiotelemetry data and state of carcass decomposition.

Covariate selection, model selection, and inferences

Examining survival rates of adults, subadults, and cubs in the reference and treatment periods allowed us to assess changes in survival that might be associated with hunting. A period (i.e., reference and treatment periods) effect would support an inference that hunting mortality was an important factor explaining the variation in puma survival. However, if models lacking the period effect received the most support, this would indicate that survival was influenced mainly by other factor(s) or that statistical power was insufficient to detect a treatment effect. Thus, we developed models with sets of covariates that we hypothesized might affect survival of adult, subadult, and cub pumas of either sex. Because selection of male pumas by hunters was evident, we also modeled adult and subadult puma survival by varying male survival by period while keeping female survival constant. We used year as a covariate for adults and month for subadults in time-varying models. Cub survival covariates also included period and whether a cub's mother lived or died during the stage of dependency. We modeled puma survival for all three life stages including constant, additive, and interactive combinations of some covariates. Reliable estimates of mule deer and elk abundances for the UPSA did not exist, thus we could not accurately estimate the effect of a prey covariate.

We evaluated the importance of candidate models in an information-theoretic approach (Burnham and Anderson 1998). For adults and subadults, we used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to rank the models. We considered models with the lowest AIC_c scores, high AIC_c weights, and models with ΔAIC_c <2 as having the most support. We report survival estimates for the top model and other supported models. We used the monthly survival rates in MARK for adults and converted them to annual survival rates (i.e., $S_{monthly}^{12}$) with 95% CIs. Likewise, we used monthly survival rates generated in MARK for subadults and converted them to life stage survival rates with 95% CIs.

For cub survival, the assumption that each radio-collared cub was an independent random sample (i.e., distribution of mortalities among litters is random) may be violated because we often collared 2−3 siblings per litter, and the fates of siblings might be linked. For example, more than 1 cub in a litter may die from the same proximate cause (e.g., infanticide) or a cub's enhanced survival may be linked to death of siblings (i.e., resulting from greater individual maternal care). Violation of the independence assumption can result in unbiased survival point estimates, but sample variances are expected to be underestimated. The data are said to be over-dispersed (Bishop et al. 2008). Therefore, we examined validity of the independence assumption in the cub data by estimating an over dispersion parameter $\hat{c}$ by following the method of Cooch and White (2015). We used the Tests option in program MARK to run 1000 bootstrap simulations on our cub data set in the most parameterized survival model we could use. We then estimated $\hat{c}$ by dividing the observed $\hat{c}$ in the original model estimate by the mean simulated $\hat{c}$. We considered $1.0 < \hat{c} \leq 1.2$ as weak evidence of over-dispersion as suggested by Bishop et al. (2008) and Ruth et al. (2011). If the results indicated non-independence in the cub fates, we used the Adjustments option for $\hat{c}$ in MARK and entered in the estimated $\hat{c}$ to adjust for the quasi-likelihood estimate ($QAIC_c$). We considered the models with the lowest $QAIC_c$ scores, high $QAIC_c$ weights, and $\Delta QAIC_c$ <2 as having the most support. Survival parameters for cubs were monthly estimates generated in MARK that we converted to life stage survival rates with 95% CIs.

Puma reproduction

Female pumas with GPS and VHF collars provided data on parturition (date), gestation (days), litter size (no.), sex of cubs observed in nurseries, birth intervals (mo.), and age at first breeding (mo.). Reproduction was verified by direct observations of cubs in nurseries and in association with adult females during capture events. We estimated ages for a sample of females when they produced the first litters that we observed. Non-productive status was assigned to females with nipples that were tiny and pink or white in color indicating no previous suckling. We reported average age, range, and 95% CIs. We estimated gestation lengths (days)

for litters from the first and last days we detected females in association with adult males by GPS- and VHF-telemetry and to the estimated dates of births and reported minimum and maximum, medians, and averages with 95% CIs.

Parturition rate, defined as the proportion of adult female pumas giving birth each year, was estimated annually from RY2 through TY5 when ≥12 adult females occurred in annual samples ($n = 4$ for RY1). We recorded whether or not individual adult females produced litters each year during the reference and treatment periods. Because the same adult females occurred in multiple samples across periods, mean period parturition rate was modeled by using the generalized linear mixed model procedure with the binomial distribution and logit link (PROC GLIMMIX) in SAS (Version 9.3, 2010, SAS Institute) where the period was the fixed effect and individual puma was the random effect.

We quantified birth intervals for adult females that we could monitor continuously by radio-telemetry. To examine variation in birth interval lengths in the reference and treatment periods, we used data from all mothers in the study except those that we knew had lost all of the cubs in their previous litter. We used individual, study period (i.e., reference, treatment), and birth interval length in months as covariates. Because some adult females occurred in multiple intervals and both periods, we analyzed birth interval as the response variable with the mixed linear model procedure (PROC MIXED) in SAS, with period as the fixed effect and individual puma as the random effect.

We examined puma litters at nurseries when the cubs were 25−45 days old. If younger cubs died before we observed them, then the litter sizes we recorded might be biased low. We coded the data by adult female, study period, and the

Chapter 4. Results

Puma capture

From 2 December 2004 to 30 October 2014, we captured as many as 256 individual pumas a total of 440 times on the UPSA. About 30 individual pumas were captured with dogs but

number of cubs observed (i.e., 1, 2, 3, 4). Adult females in the samples gave birth multiple times within the same period and in both periods, therefore, we modeled period mean litter size using the mixed linear model procedure (PROC MIXED) in SAS, where period was the fixed effect and individual puma was the random effect. Normal distribution error structure was used for this analysis and assumptions of normality were met. We examined the proportions of male and female nurslings we observed in litters in each study period and the entire study by calculating the binomial proportions and Clopper-Pearson exact 95% CIs by using the PROC FREQ procedure in SAS. Inferences on period effects on parturition rate (on the logit scale), birth interval, litter size, and proportions of the sexes in litters were made by examining the 95% CIs on the differences of the estimates for each period by using the delta method (Seber 1982).

Puma hunters
Data on puma hunters were compiled from the surveys that hunters returned. We report ranges and medians for repetitious response values (e.g., number of days hunted). Estimates on number of hunters that actually hunted on the study area each treatment year were the number of hunters requesting permits to hunt UPSA multiplied by the proportion of the hunters that indicated they hunted on UPSA. We counted the number of male and female puma tracks <1 day old when first encountered by hunters and researchers, male and female independent pumas killed and caught and released by hunters and that were in the LP estimates pre-harvest and post-harvest each treatment year, and report them as male:female ratios. The ratios were used to discern risk to pumas of either sex to detection by hunters and evidence of selection by hunters.

not handled and marked at that time due to their dangerous positions in trees or on cliffs. Of those, 11 were captured in the reference period, of which 6 were associated with marked family members (i.e., mothers or siblings). In the treatment period, 19 pumas were not handled, and 8 of those were associated with marked family members. It is possible, however, that we captured and marked some of those individuals

at later dates in the study, which would reduce the total number of individual pumas we captured. The number of days we spent each winter searching for pumas with dogs was similar in each period (reference mean = 77, range 71−82; treatment mean = 79, range 74−86). However, in RY5 (i.e., 2008−2009) a Colorado state government-mandated hiring freeze resulted in insufficient personnel for thorough searches of the study area and a substandard effort to detect pumas. No adult or subadult pumas died from capture procedures. One cub was killed by our tracking dogs. Three cubs died as a result of premature expansions of the radiocollars: 1 nursling starved because the transmitter was caught in its mouth; 2 cubs died after they passed a foreleg through the collar, causing one to starve because it could not keep up with movements of its family, and the other to die apparently of infection after the collar material cut into the axilla.

We uniquely marked 226 pumas, 110 in the reference period and 116 in the treatment period. The number of radio-collared pumas monitored each year ranged from 16 to 56 and averaged 40. Marked pumas provided known-fate data on 75 adults, 75 subadults, and 118 cubs. Some cubs and subadults transitioned to older stages, which is why the total number of marked pumas in the life stage classes (268) is greater than the total

pumas marked. By the end of the study, we accounted for the fates (i.e., pumas either survived or died) of all of the radio-collared adults, including those with failed radiocollars, except for one female and one male. We lost track of the female in TY2 when her collar stopped functioning while she was in a part of her home range outside the UPSA. We lost track of the male when his collar stopped functioning in TY5.

Causes of mortality in independent pumas

In the reference period, the hunting closure on the UPSA and protection of marked pumas in adjacent GMUs to the north effectively eliminated hunting mortality in marked adults of both sexes and subadult females (Fig. 4A). Over twice as many adult pumas died of natural causes (i.e., intraspecific killing, other causes) than adults that died from other human causes (i.e., vehicle strikes, depredation control). A majority (i.e., 6 of 10) of the independent pumas that died were adult females, with the remainder comprised of adult males and subadults. One adult male was killed by another male puma. Two subadult female deaths occurred, 1 each from a vehicle strike and trampling by an elk. One subadult male was harvested in a GMU adjacent to the UPSA.
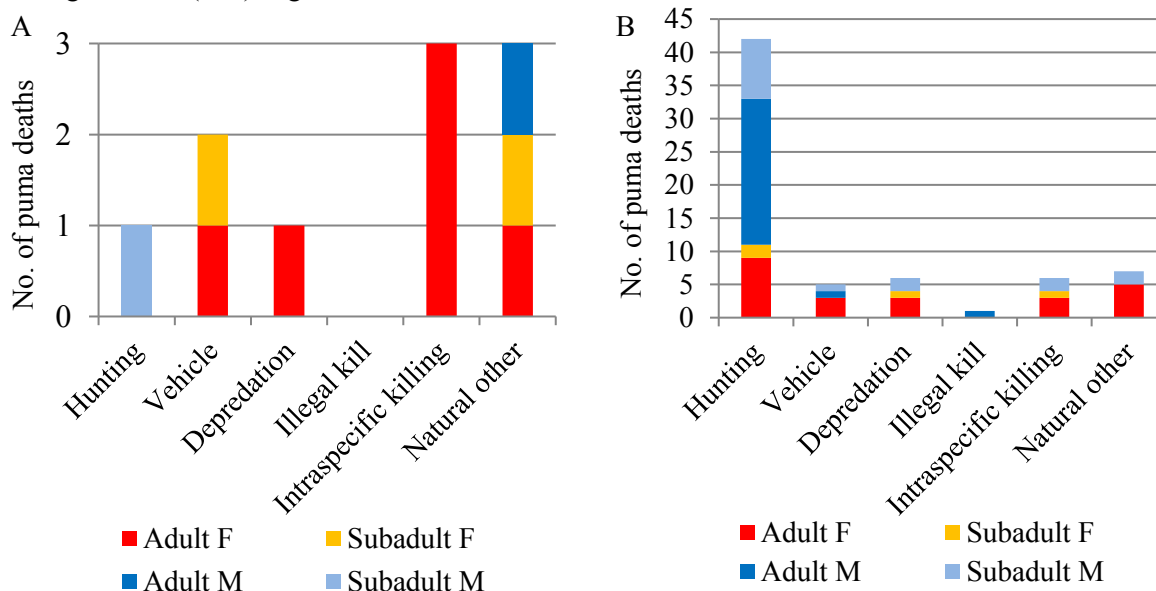
Figure 4. Proximate causes of death in marked adult and subadult pumas during the reference period (A) and the treatment period (B), 2004−2014, on the Uncompahgre Plateau Study Area, Colorado, USA.

In the treatment period, human-causes, hunting in particular, were the most important sources of death for marked adult and subadult pumas, comprising 65% and 100% of adult female and male mortalities, respectively, and 75% of both subadult female and male mortalities (Fig. 4B). Adult females in particular (i.e., 35% of their deaths), and to a lesser extent subadult pumas, continued to die of natural causes. An 11-year-old female that died of starvation apparently in association with senescence was the only independent puma we found that succumbed to starvation during our entire study.

Adult female puma F104 died of starvation associated with senescence, January 2012. © CPW PHOTO.

Hunting treatment and other mortality

A harvest quota of 8 pumas on the UPSA during TY1−TY3 resulted in 9 pumas harvested in TY1 and 8 pumas harvested in each season TY2 and TY3 (Table 1). Harvest rates based on the LP $\hat{N}_c$ estimates (Table 2) of independent pumas on the UPSA for years TY1−TY3 averaged 16% (Table 3). After we reduced the quota to 5 pumas for TY4 and TY5, hunters killed 5 animals in each of those seasons. In TY4 and TY5, the UPSA-specific harvest rates averaged 13%. Male pumas comprised 69% and adult males 46% of the total 35 pumas harvested on the UPSA during TY1−TY5. Females comprised 31% and adult females 23% of the total harvest. The estimated average age of all the pumas harvested on the UPSA during the treatment period was 3.5 years (range 1.1−9.5).

Table 1. Numbers of independent pumas harvested annually during treatment period hunting seasons on the Uncompahgre Plateau Study Area (UPSA) and additional independent pumas with home ranges overlapping the UPSA harvested on adjacent Game Management Units (in parentheses), treatment year 1 (TY1) to treatment year 5 (TY5), 2009−2014, Colorado, USA.

Treatment year	Adult		Subadult		Quota	Total no. pumas harvested
	Female	Male	Female	Male		
TY1	2 (1)	5 (4)	1	1	8	9 (5)
TY2	0	5 (1)	2	1	8	8 (1)
TY3	3	1 (2)	0	4	8	8 (2)
TY4	2 (1)	2 (1)	0 (1)	1	5	5 (3)
TY5	1	3	0	1	5	5
Subtotals	8 (2)	16 (8)	3 (1)	8		

Table 2. Lincoln-Petersen parameter counts, pre-hunting abundance estimates ($\hat{N}_c$) and 95% Confidence Intervals (CI) of independent pumas during winter[a] from reference years 2−5 (RY2−RY5) and treatment years 1−5 (TY1−TY5), 2005−2014, Uncompahgre Plateau Study Area, Colorado, USA.

Study Winter	n_1[b]	n_2[c]	m_2[d]	$\hat{N}_c$ estimate[e]	95% CI	Detection probability[f]
RY2	9	18	7	23	18−28	0.78
RY3	16	22	11	32	25−39	0.69
RY4	17	29	15	33	29−37	0.88
RY5	20	25	12	41	31−51	0.60
TY1	32	48	27	57	52−62	0.84
TY2	29	50	26	56	51−61	0.90
TY3	23	40	21	44	40−48	0.91
TY4	21	37	18	43	38−48	0.86
TY5	21	32	18	37	33−41	0.86

[a]Each entire capture and hunting season (Nov−Mar) was treated as a sampling period.
[b]n_1 is the number of marked independent pumas expected to be in the UPSA at the start of the sampling period (i.e., Nov).
[c]n_2 is the total number of independent pumas physically captured, detected by radiotelemetry, and back-aged into the sampling period.
[d]m_2 is the number of independent pumas detected during the sampling period in the n_2 sample that was previously marked.
[e] $\hat{N}_c$ estimate is pre-harvest abundance in November.
[f] Detection probability = m_2 / n_1.

Table 3. Puma mortality rates based on adult and subadult pumas that died on the Uncompahgre Plateau Study Area (UPSA) and with additional adult and subadult pumas with home ranges that overlapped the UPSA that died on adjacent GMUs (in parentheses) expressed as a proportion of Lincoln-Petersen $\hat{N}_c$ estimates during hunting seasons from treatment year 1 (TY1) to treatment year 5 (TY5), 2009−2014, Colorado, USA.

Treatment year	Puma harvest rate	Total human-caused puma mortality rate	Total puma mortality rate
TY1	0.16 (0.25)	0.16 (0.25)	0.16 (0.25)
TY2	0.14 (0.16)	0.18 (0.20)	0.18 (0.20)
TY3	0.18 (0.23)	0.18 (0.23)	0.23 (0.27)
TY4	0.12 (0.19)	0.12 (0.19)	0.14 (0.21)
TY5	0.14	0.14	0.16

Six other independent pumas died of causes other than hunting on the UPSA during the hunting seasons, ranging from 0−2 deaths each season; all were adult females (Table 4). With these deaths added to the harvest on the UPSA, total UPSA mortality rates during TY1−TY3 averaged 19% (Table 3). In TY4 and TY5 total UPSA mortality rates averaged 15%. However, 4 of the 6 adult females died of natural causes on the UPSA. Just counting the human-caused deaths on UPSA that would have been detected by wildlife managers (i.e., harvest and depredation control) the total UPSA human-caused mortality during TY1−TY3 averaged 17%. In TY4 and TY5 the total UPSA human-caused mortality rate averaged 13%.

Table 4. Numbers of adult and subadult pumas that died of all causes on the Uncompahgre Plateau Study Area (UPSA) and adult and subadult pumas with home ranges that overlapped the UPSA that died on adjacent GMUs (in parentheses) during hunting seasons from treatment year 1 (TY1) to treatment year 5 (TY5), 2009−2014, Colorado, USA.

Treatment year	Hunting	Vehicle strike	Depredation control	Natural	Total mortalities
TY1	9 (5)	0	0	0	9 (5)
TY2	8 (1)	0	2	0	10 (1)
TY3	8 (2)	0	0	2	10 (2)
TY4	5 (3)	0	0	1	6 (3)
TY5	5	0	0	1	6
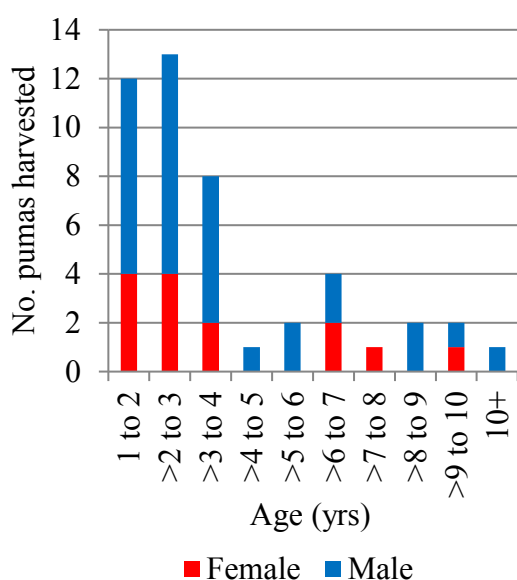
Figure 5. The age structure of pumas harvested on the Uncompahgre Plateau Study Area (UPSA) and pumas with home ranges overlapping the UPSA that were harvested on adjacent Game Management Units, 2009−2014, Colorado, USA.

In addition, hunters killed 11 other radio-collared independent pumas (2 adult females, 8 adult males, 1 subadult female) in adjacent GMUs 61, 62, 65, and 70 that had home ranges overlapping the UPSA boundaries (Table 4). Two of the adult radio-collared males were trailed by hunters' dogs off of the UPSA and were caught and killed in adjacent GMUs 65 and 70. Including these pumas, harvest rates as a percentage of the LP $\hat{N}_c$ estimates averaged 21% for TY1−TY3 and 17% in TY4 and TY5. Also, when including these cases, total human-caused mortality (range 19−25%) and total puma mortality rates (range 21−27%) increased during TY1−TY4, but not in TY5 (Table 3). Of the 46

pumas that used the UPSA and were harvested during TY1−TY5, males comprised 70% and adult males 53%. Females comprised 30% and adult females 22% of the total harvest. The estimated average age of all the pumas harvested was 3.8 years (range 1.1−10.1). Of those, 26% were subadults, 48% were adults >2−5 years old, and 26% were adults >5 years old (Fig 5).

All marked adult pumas that died from hunting (7 females, 14 males) and depredation control (3 females) were detected by, or reported to, wildlife managers. However, 18 adult puma deaths, including 15 natural deaths (14 females, 1 male), an illegal kill (1 male), and 2 (both females) of 4 vehicle strike deaths (3 females, 1 male) were not detected by wildlife managers but instead by our radiotelemetry monitoring. All marked subadult puma deaths from hunting (2 females, 10 males), depredation control (1 female, 2 males), and vehicle strikes (1 female, 1 male) were detected by, or reported to, managers. But managers detected only 1 (male) of 6 subadult puma deaths (2 females, 4 males) due to natural causes.

Of 55 radio-collared cubs (28 females, 27 males) monitored in the reference period, 18 died (Table 5). Of those, 72% died when ≤5 months old. Natural causes dominated deaths of cubs (94.4%), of which infanticide was the greatest single cause (72.2%). Human-caused cub deaths were 5.6%. Four non-collared cubs also died, including 1 litter of 3 nurslings that starved to death after the mother was killed for depredation control, and 1 ear-tagged cub that died of infanticide when the mother was also killed by a male puma.

Of the 63 radio-collared cubs (27 females, 36 males) monitored in the treatment period, 27

died (Table 5). Of those, 80% died when ≤5 months old. Natural mortality comprised the majority of cub deaths (55.6%). The greatest proximate mortality cause was starvation including: 3 cubs of 2 mothers that died of natural causes, 3 cubs of 2 mothers killed by hunters, and 3 cubs of 1 mother killed for depredation control. The 6 cubs that starved because their mothers died from anthropogenic causes comprised 22.2% of the cubs that died. Infanticide deaths declined to 29.6%, and human-caused cub deaths increased to 44.4%. In addition, we observed mortality in 3 litters of non-collared cubs: 2 litters (1 with 2 cubs and 1 with ≥1 cubs) died of infanticide, and the third

litter (with ≥1 cub) died due to black bear predation.

Infanticide caused 13 cub deaths in 8 of 32 radio-monitored litters in the reference period. This included 1 litter of 3 cubs killed 1−8 days after the mother was killed by vehicle strike. In the treatment period 8 cubs in 5 of 45 radio-monitored litters died of infanticide. The proportion of litters subject to infanticide in the reference period tended to be higher (0.25, 95% CI = 0.12−0.43) than in the treatment period (0.11, 95% CI = 0.04−0.24), but the 95% CI (−0.04−0.32) on the difference included zero.

Table 5. Mortality causes and amount by sex and period (No., %) and total by period (No., %) of radiocollared puma cubs during the reference (n = 28 F, 27 M) and treatment (n = 27 F, 36 M) periods, 2004−2014, Uncompahgre Plateau Study Area, Colorado, USA.

Study period	Mortality cause	No. F (%)	No. M (%)	Total No. (%)
Reference	Infanticide	9 (64.3)	4 (100)	13 (72.2)
	Predation	1 (7.1)	0 (0)	1 (5.6)
	Unknown natural	3 (21.4)	0 (0)	3 (16.7)
	Vehicle strike	1 (7.1)	0 (0)	1 (5.6)
Treatment	Infanticide	3 (30)	5 (29.4)	8 (29.6)
	Unknown natural	0 (0)	4 (23.5)	4 (14.8)
	Natural starvation	1 (10)	2 (11.8)	3 (11.1)
	Human-caused starvation	4 (40)	2 (11.8)	6 (22.2)
	Vehicle strike	0 (0)	2 (11.8)	2 (7.4)
	Depredation control	2 (20)	1 (5.9)	3 (11.1)
	Mauled by hunter's dogs	0 (0)	1 (5.9)	1 (3.7)

Abundance, population growth, and mortality in independent pumas

The LP $\hat{N}_c$ estimates of independent pumas that used the UPSA increased in the reference period from 23 in RY2 to 57 in TY1 (Table 2, Fig. 6) at median observed finite growth rates (λ) ranging from 1.04 (RY3−RY4) to 1.39 (RY2−RY3 and RY5−TY1; Table 6). In the treatment period, estimated abundance of independent pumas on the UPSA declined from 57 in TY1 to 37 in TY5. The geometric mean of λ shows an

average 10% decline in abundance each year. Non-marked pumas captured for the first time or harvested when ≥3 years old and used to adjust n_2 data in previous years for LP estimates included 11 females (average age = 4.5 yr., 95% CI = 3.5−5.5) and 13 males (average age = 3.8 yr., 95% CI = 3.3−4.3).

Estimated abundance of independent pumas that ranged on the UPSA declined 23% between TY1 and TY3 (Table 2) after an average 15% harvest on the UPSA in TY1 and TY2 (Table 3, Fig. 6).
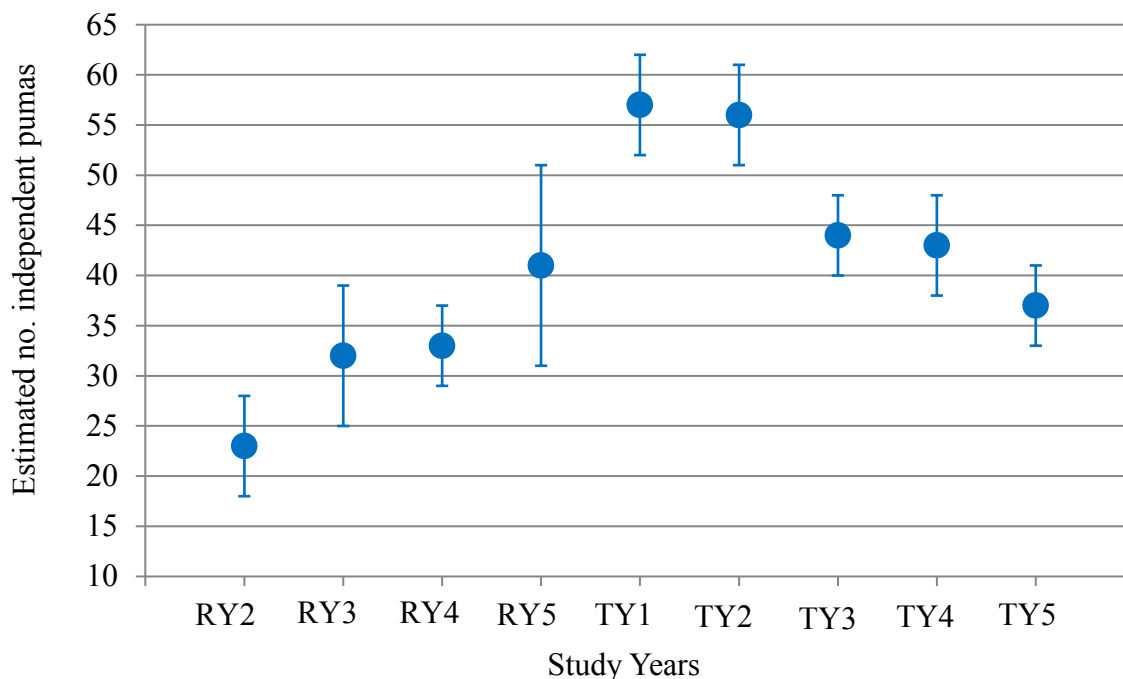
Figure 6. Lincoln-Petersen estimates (dots) with 95% Confidence Intervals (bars) of independent pumas that used the Uncompahgre Plateau Study Area each winter, reference year 2 (RY2) to treatment year 5 (TY5), 2005−2014, Colorado, USA.

Table 6. Estimated finite growth rates (λ) and lower and upper 95% Confidence Limits (LCL, UCL) of independent puma abundance, reference years 2−5 (RY2−RY5) and treatment years 1−5 (TY1−TY5), 2005−2014, based on Lincoln-Petersen estimates ($\hat{N}_c$) of independent pumas in winter, Uncompahgre Plateau Study Area, Colorado, USA.

	λ		
Interval	Median	95% LCL	95% UCL
RY2−RY3	1.39	1.01	1.94
RY3−RY4	1.04	0.83	1.34
RY4−RY5	1.25	0.94	1.58
RY5−TY1	1.39	1.10	1.82
TY1−TY2	0.98	0.87	1.12
TY2−TY3	0.79	0.70	0.88
TY3−TY4	0.98	0.85	1.13
TY4−TY5	0.87	0.74	1.02

In total, estimates of independent pumas that ranged on the UPSA declined 35% by TY5 following four hunting seasons (TY1−TY4) in which annual harvest rates on the UPSA averaged 15%. For the population declines measured by TY3 and TY5 (i.e., the 95% CIs on the estimates for TY3 and TY5 do not overlap with the 95% CIs of the estimate for TY1), the total human-caused mortality rates on the UPSA averaged 17% and 16%, respectively, and the UPSA total mortality rates averaged 19% and 18%, respectively. Including the radio-collared pumas with home ranges overlapping the UPSA that were harvested on adjacent GMUs, harvest rates averaged 21% during TY1−TY4 (Table 3). For the population declines measured by TY3 and TY5, the total human-caused mortality rates on the UPSA averaged 23% and 22%, respectively, and the UPSA total mortality rates averaged 24% and 23%, respectively.
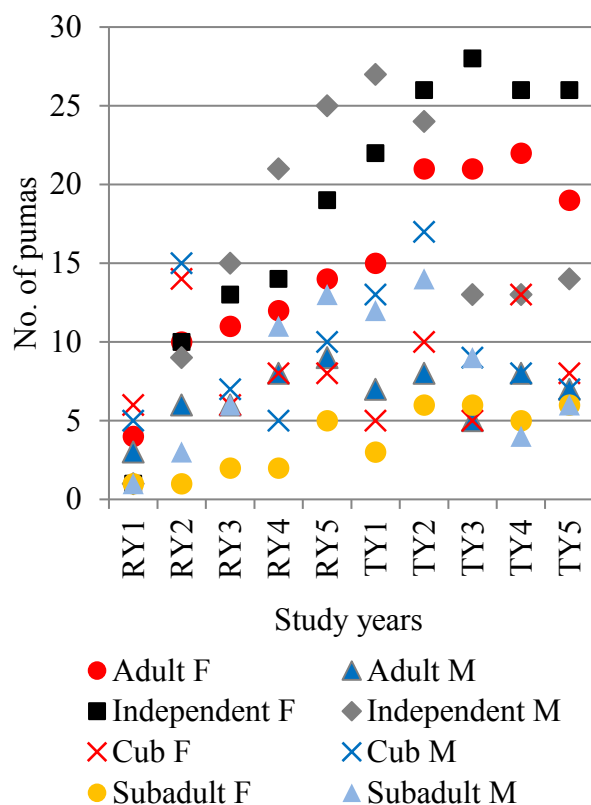
Figure 7. Numbers of marked adult, subadult, and cub pumas monitored for survival and mortality estimates, and independent pumas (i.e., adults and subadults) monitored for multinomial analysis of cause-specific mortality rates, reference year 1 to treatment year 5 (RY1−TY5), 2004−2014, on the Uncompahgre Plateau Study Area and bordering Game Management Units, Colorado, USA.

Our multinomial analysis of fates of marked independent pumas at the "population-scale" included 19−44 pumas annually from RY2−RY5 and 39−50 annually TY1−TY5 (Fig.7). Of those, 35 females and 42 males died, including 11 females and 33 males that were harvested, all of them in the UPSA and 4 bordering management units (i.e., GMUs 61, 62, 65, 70) managed for stable or increasing puma population objectives (Fig. 8). Only 0−2% of the marked independent pumas with known fates were harvested annually during the reference period (Table 7). One subadult male was harvested in a GMU adjacent to the UPSA in RY5. In contrast, annual harvest rates increased in the treatment period from 13−27%. Population-scale harvest rates for years TY1−TY4 averaged 22% (Table 7), and by TY5 the estimated abundance of

independent pumas on the UPSA declined by 35%. Females and adult females comprised 26% and 21%, respectively, of the total number of marked pumas harvested during TY1−TY5. Other human-caused mortality averaged 2% annually in the reference period and 5% annually in the treatment period. Total annual human-caused mortality rates averaged 3% in the reference period and increased to 25% in the treatment period. Natural mortality rates averaged 5% annually in the reference period and 6% in the treatment period. Total annual mortality rates averaged 8% in the reference period and increased to 31% in the treatment period. Marked independent pumas that emigrated from the UPSA and adjacent GMUs averaged 8% annually in the reference period and 4% annually in the treatment period with broadly overlapping confidence intervals (Table 7).

Puma sex and age structure
The puma sex and age structure on the UPSA in winter, based on LP estimates of adult female, male, and subadult pumas indicated that adults were more abundant than subadults every year (Table 8). In the reference period, adult females were in parity with adult males during RY2−RY3 when the abundance of independent pumas was lowest. As the abundance of adult pumas increased to the beginning of TY1, adult females became more numerous than adult males by ratios ranging from 1.2:1−1.9:1. During the treatment period, ratios of adult females to males diverged further, ranging from 1.2:1−3:1, with the widest margins during TY3−TY5 when the population declined again to a low phase. Subadult females occurred slightly more than males (i.e., 29 females: 25 males, Fig. 9) throughout the study. Cubs outnumbered subadults every year, and generally numbered less than adults (Table 8).

During the reference period, we found relatively few pumas 1−2 years old, and there were over twice as many females as males (Fig 9). In the first 2 years of the reference period adult pumas >5 years old were few (Fig. 9, RY1, RY2). The number of pumas >5 years old increased, however, during RY3 to the beginning of TY1 as the population on the UPSA increased.

Table 7. Population-scale estimated puma agent-specific mortality rates and emigration rates (with 95% Confidence Intervals) for marked adult and subadult pumas with known fates from multinomial analysis of reference years 2−5 (RY2−RY5) and treatment years 1−5 (TY1−TY5), 2005−2014, Uncompahgre Plateau Study Area and adjacent Game Management Units, Colorado, USA.

Study Year	Hunting mortality	Other human-caused mortality	Natural mortality	Population-scale emigration[a]	Total human-caused mortality	Total mortality
RY2	0	0	0.05 (0.01-0.31)	0.05 (0.01-0.31)	0	0.05 (0.01-0.31)
RY3	0	0	0.07 (0.02-0.28)	0.07 (0.02-0.28)	0	0.07 (0.02-0.28)
RY4	0	0.03 (0.00-0.20)	0.06 (0.01-0.24)	0.14 (0.05-0.34)	0.03 (0.00-0.20)	0.09 (0.02-0.26)
RY5	0.02 (0.00-0.17)	0.05 (0.01-0.20)	0.02 (0.00-0.17)	0.05 (0.01-0.20)	0.07 (0.02-0.23)	0.09 (0.03-0.25)
TY1	0.22 (0.11-0.40)	0.04 (0.01-0.18)	0.04 (0.01-0.18)	0.06 (0.02-0.21)	0.27 (0.14-0.44)	0.31 (0.18-0.48)
TY2	0.14 (0.06-0.31)	0.10 (0.03-0.26)	0.10 (0.03-0.26)	0.08 (0.02-0.23)	0.24 (0.12-0.41)	0.34 (0.20-0.51)
TY3	0.27 (0.13-0.47)	0.02 (0.00-0.18)	0.07 (0.02-0.25)	0.05 (0.01-0.21)	0.29 (0.15-0.49)	0.37 (0.21-0.55)
TY4	0.23 (0.11-0.43)	0.05 (0.01-0.22)	0.03 (0.00-0.18)	0	0.28 (0.15-0.47)	0.31 (0.17-0.49)
TY5	0.13 (0.04-0.31)	0.03 (0.00-0.18)	0.08 (0.02-0.25)	0.03 (0.00-0.18)	0.15 (0.06-0.34)	0.23 (0.11-0.42)

[a]Population-scale emigration rates refer to marked subadult pumas that moved beyond the boundaries of the Uncompahgre Plateau Study Area and bordering Game Management Units.
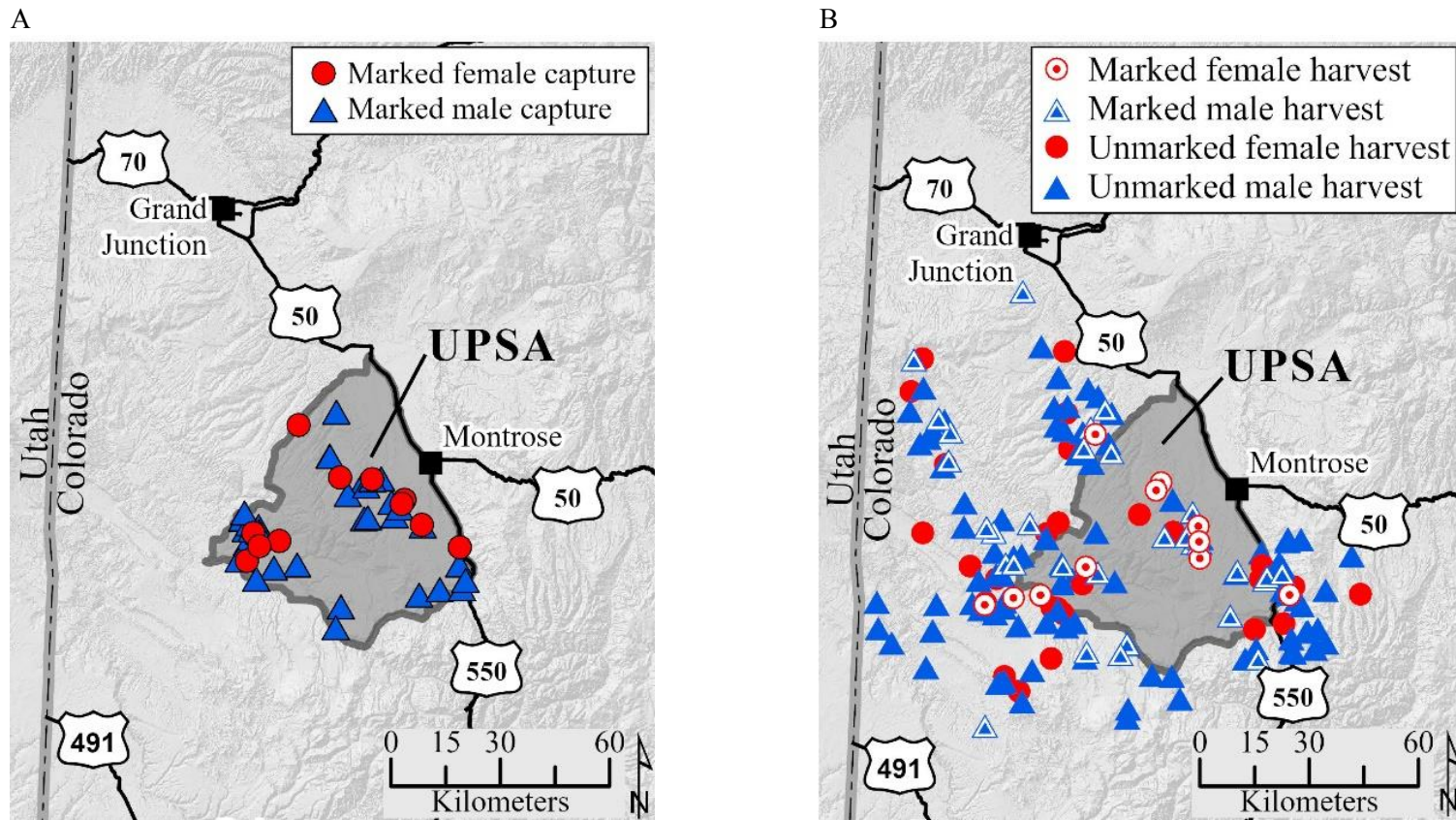
Figure 8. Initial capture locations of marked independent pumas (A) and harvest locations of marked and unmarked independent pumas (B) that were either harvested on the Uncompahgre Plateau Study Area (UPSA) or adjacent Game Management Units during the treatment period, 2009−2014, Uncompahgre Plateau, Colorado, USA.

The broadest age distribution for both sexes occurred at the start of the treatment period and after 5 years of no hunting (i.e., TY1, Fig. 9). Pumas 1−5 years old comprised 66% of the independent animals; the other 34% were adult females and males >5−10+ years old (Fig. 9, TY1). In TY1, adult males >5−10+ years old comprised 43% of the adult males. Estimated winter abundance of adult males declined by 59% between TY1 and TY4 and remained as low in TY5 (Table 8). After 2 years of hunting, adult males >6 years old were absent from the sampled winter sex and age structures (TY3−TY5, Fig. 9, D). There were more pumas 1−2 years old tallied each year in the treatment period than each year in the reference period. Also, there were almost as many females (i.e., 21) as males (i.e., 23) 1−2 years old throughout the treatment period.

Table 8. Lincoln-Petersen winter estimates and 95% Confidence Intervals (CI) of adult female, male and subadult (sexes combined) pumas[a], and counts of cubs[b] (sexes combined), reference years 2−5 (RY2−RY5) and treatment years 1−5 (TY1−TY5), 2005−2014, Uncompahgre Plateau Study Area, Colorado, USA.

Study year	Adult females	95% CI	Adult males	95% CI	Subadults	95% CI	Cubs
RY2	11	8−14	10	6−14	2	2−2	14
RY3	16	13−19	15	8−22	1	1−1	16
RY4	19	16−21	10	9−12	3	3−3	20−21
RY5	24	16−32	13	10−16	5	0−10	21
TY1	26	22−29	22	19−25	9	7−11	19−24
TY2	28	27−30	18	15−21	10	10−10	39
TY3	23	21−24	10	10−10	10	10−10	19
TY4	27	23−31	9	9−9	6	6−6	24
TY5	19	17−20	9	7−11	9	9−9	25−28

[a]Numbers of adults and subadults deviate by 1 animal from estimates of independent pumas in Table 2 due to rounding errors for RY4, RY5, TY3, and TY4.
[b]Includes cubs observed with mothers and cubs counted by tracks associated with mothers.

After the first 2 years of hunting in the treatment period, adult males >6 years old, such as this one examined by Ken Logan, were absent from the sampled winter puma population. © CPW PHOTO.
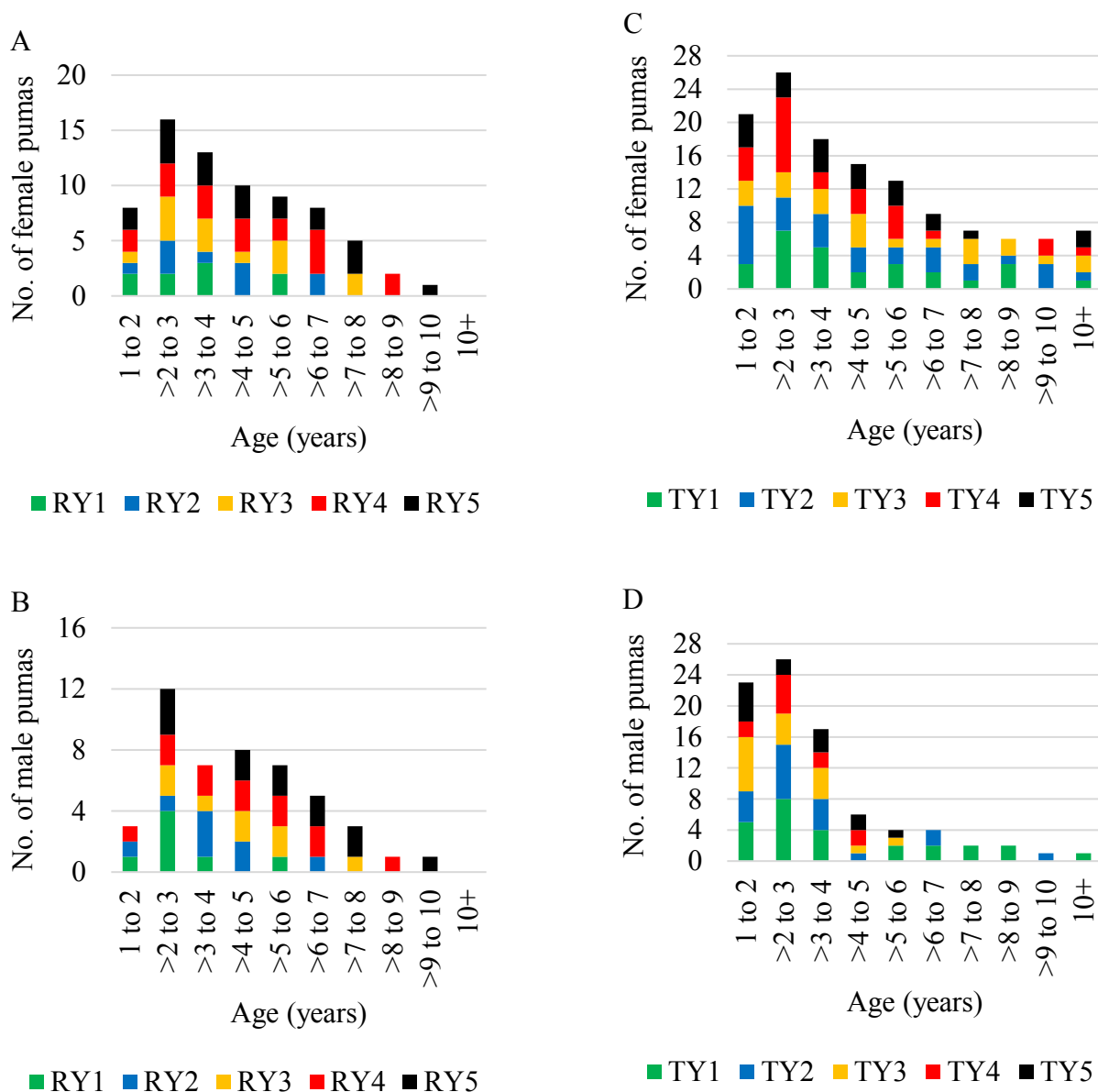
Figure 9. Sex and age structure of adult and subadult pumas that were captured, harvested, and examined in the reference and treatment periods, 2004−2014, on the Uncompahgre Plateau Study Area, Colorado, USA. Females and males in panels A and B, respectively, in reference period years RY1−RY5. Females and males in panels C and D, respectively, in treatment period years TY1−TY5.

Estimated adult female abundance was generally stable from TY1−TY4, but declined to its lowest in TY5 (Table 8). The difference in the TY4 and TY5 adult female estimates could mostly be explained by 5 adult females that died during TY4 (2 harvested on the UPSA, 1 harvested adjacent to the UPSA, 1 died of natural cause, 1 died of vehicle strike) and 1 adult female that stayed on a portion of her home range outside the UPSA after June in TY4. In addition, 2 adult females caught in TY5 with home ranges that overlapped the UPSA were back-aged into the TY4 estimate. We could not directly account for other non-marked adult females estimated in TY4 that might have died before TY5 or had overlapping home ranges with the UPSA. Adult female age distribution was relatively even from TY1−TY3; but adult females >6 years old declined during TY4 and TY5 (TY1−TY5, Fig. 9, C).

At the beginning of RY1 independent males averaged 2.7 years old (95% CI = 1.8−3.7). Similarly, independent females averaged 3.3 years old (95% CI = 2.3−4.2). By the beginning of TY1 independent males averaged 4.2 years old (95% CI = 3.1−5.2), similar to the average of 4.4 years for independent females (95% CI = 3.4−5.3). By the start of TY5 the average age of independent males was 2.9 years old (95% CI = 2.1−3.7), indicative of the declining male age structure. Independent females at the start of TY5 averaged 4.5 years old (95% CI = 3.3−5.7), similar to TY1.

Puma philopatry, dispersal, and emigration

We estimated age (months) of transition from the cub to subadult stage for 15 radio-collared pumas (11 males, 4 females). They became independent at a median age of 13.0 months (average = 13.7, range 9−16). Ten pumas (8 males, 2 females) dispersed from natal areas at a median age of 14.5 months (average = 15.5 months, range 10−22) and during April to October. Seven of those (5 males, 2 females) dispersed from natal areas before their first winter in the subadult stage, and all except for 1 female emigrated from the UPSA.

Seven marked pumas born on the study area that survived to adult ages exhibited philopatry. Five females established adult home ranges overlapping their mothers'; 4 of those subsequently reproduced. One male was killed by a hunter within his mother's home range when he was 30 months old. We recaptured another male when he was 28 months old, 1.8 km north of this mother's home range; 1 week later he was killed by a hunter 3 km north of his mother's home range. Because of the short time he wore a radiocollar as an adult we could not determine the extent his movements overlapped with his mother's home range. Both males may have also ranged off of the study area, as did their mothers, after their cub collars quit functioning and we could no longer monitor their movements. Both of the males died 11.1 and 12.8 km from the nurseries where they were initially marked.

Of 37 cubs surviving to the subadult stage in the reference period at least 10 (9 males, 1 female) or 27% were known to have emigrated from the

UPSA. Similarly, of 36 cubs surviving to subadult stage in the treatment period at least 9 (8 males, 1 female) or 25% were known to have emigrated from the UPSA.

We collected data on 34 pumas (7 females, 27 males) that were born on the UPSA and dispersed from natal areas (Fig. 10). Four females and 24 males emigrated entirely from UPSA. Females dispersed an average of 30.7 km (95% CI = 23.2−38.2, range 18.7−46.8). Dispersal endpoints for females were determined when they were 17−44 month old (average = 26.7, 95% CI = 24.7−28.8). Males dispersed longer distances than females, averaging 63.9 km (95% CI = 53.8−74.0, range 17.7−104.1). Dispersal endpoints for males were determined when they were 17−65 months old (average = 33.1, 95% CI = 27.8−38.3).
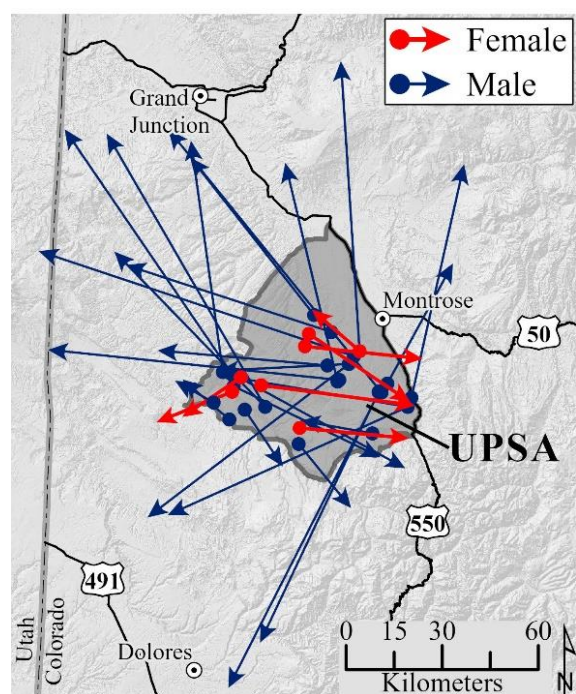
Figure 10. Pumas born, captured, and marked on the Uncompahgre Plateau Study Area (UPSA) Colorado, USA, 2004−2014, that later dispersed from their natal areas after separation from mothers. End points of their movements indicated by the ends of the arrows are to the last known locations.

We obtained data on 14 other independent pumas (8 females, 6 males) with unknown origins which were initially captured and marked on the UPSA but subsequently emigrated (Fig. 11). At their first capture,

estimated ages of females averaged 21 months (95% CI = 17−26) and males averaged 21 months (95% CI = 17−25). Females moved on average 70.9 km (95% CI = 21.4−119.2, range 18.4−214.1) from capture sites to endpoints. We found endpoints for the females when they were about 24−79 months old (average = 33 mo., 95% CI = 20−46). Males moved on average 190.5 km (95% CI = 76.4−304.6, range 39.6−369.1) from capture sites to endpoints. Males were about 26−55 months old (average = 39, 95% CI = 29−49) when we determined their endpoints. Pumas from this group made the farthest movements with 1 female and 1 male moving to northern New Mexico, 1 male moving to the eastern slope of the Rocky Mountains in Colorado, and 1 male moving to southern Wyoming.
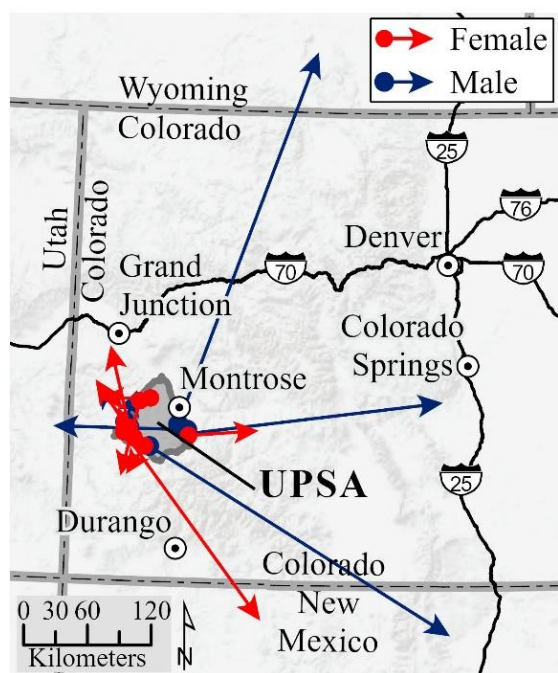
Figure 11. Pumas of unknown origin captured and marked on the Uncompahgre Plateau Study Area (UPSA), Colorado, USA, 2004−2014, that later dispersed to locations outside of the UPSA. End points of their movements indicated by the ends of the arrows are to the last known locations.

Puma survival

Adults
The adult puma survival data included 75 radio-collared individuals, with 32 (21 females, 11 males) monitored in the reference period and 61 (39 females, 22 males) monitored in the treatment period. Sixteen (10 females, 8 males) were monitored in both periods. The number of adult females and males monitored annually ranged from 10−22, and 6−9, respectively (Fig. 7). Survival modeling resulted in 2 closely ranked models with <2 ΔAIC_c units that accounted for 89% of the model weights. The top-ranked model indicated a period effect interacting with sex (i.e., Sex × Period; **Appendix III**, Table AIII. 1). Adult male annual survival was over 2 times higher in the reference period (0.96, 95% CI = 0.75−0.99) than in the treatment period (0.40, 95% CI = 0.22−0.57; Table 9). The estimate for annual adult female survival was higher in the reference period (0.86, 95% CI = 0.72−0.94) than in the treatment period (0.74, 95% CI = 0.63−0.82). The evidence ratio from AIC_c weights indicated the top-ranked model had 1.2 times the support of the second-ranked model with adult male survival interacting with period and adult female survival constant [i.e., M × period (Fconstant)]. In this model adult male annual survival varied in each period as in the top model, and adult female annual survival was 0.78 over both periods. The remaining 7 models in the 9-model candidate set had weak to no support with >4 ΔAIC_c units.

Subadults
The subadult survival sample included 75 individuals with known-fates: 22 (8 females, 14 males) in the reference period and 53 (19 females, 34 males) in the treatment period. The number of subadult females and males monitored annually ranged from 1−6, and 1−14, respectively (Fig. 7). Survival modeling resulted in 2 closely ranked models with <2 ΔAIC_c units that accounted for 77% of the model weights (**Appendix III**, Table AIII. 2). The top-ranked model indicated period as an important factor explaining male survival and with female survival constant [i.e., M × period (Fconstant)]. Subadult male survival was 2 times higher in the reference period (0.92, 95% CI = 0.57−0.99) than in the treatment period (0.43, 95% CI = 0.25−0.60). Subadult female survival was 0.68 (95% CI = 0.43−0.84) over the two periods (Table 9). The evidence ratio from AIC_c weights indicated that the top model had 2.6 times the support of the second-ranked model of sex

interacting with period (i.e., Sex × Period). Subadult male survival varied in the two periods the same as in the top model, and subadult female survival was variable but similar in the reference (0.63) and treatment (0.70) periods. The remaining 7 models in the 9-model candidate set had weak to no support with >2 ΔAIC_c units.

Cubs

The cub survival data included 118 radio-collared cubs: 55 cubs (28 females, 27 males) from 32 litters in the reference period, and 63 cubs (27 females, 36 males) from 45 litters in the treatment period. The number of cub females and males monitored annually ranged from 5−14, and 5−17, respectively (Fig. 7). The estimated $\hat{c}$ for the most parameterized cub survival model we could use (i.e., Period × Sex) was 1.55, indicating that the fates of siblings were not independent. We documented numerous occasions of this phenomenon. In the reference period 7 radio-collared siblings in 3 litters died at the same time due to infanticide. In addition 3 non-collared cubs in 1 litter starved after the mother was killed for depredation control. In the treatment period 19 radio-collared siblings in 8 litters died at the same time due to a variety of causes, including: depredation control (3 cubs in 1 litter), vehicle strike (2 cubs in 1 litter), infanticide (7 cubs in 3 litters), and starvation (7 cubs in 3 litters). In addition, 2 non-collared cubs in 1 litter died from infanticide.

Modeling results indicated 4 models with <2 $\Delta QAIC_c$ units with the covariate for mother status alive or dead (i.e., MotherId) accounting for 78% of the model weights (**Appendix III**, Table AIII. 3). These models indicated that survival of the mother during cub dependence was the most important factor to cub survival. Evidence ratios using $QAIC_c$ weights indicated the top model with the covariate MotherId alone had 2.5 times the support of the second-ranked model Sex + MotherId, and 2.7 times the support of the third- and fourth-ranked models Period + MotherId and Sex × Period + MotherId, respectively. In the top model, the survival estimate of cubs with living mothers (0.51, 95% CI = 0.35−0.66) was over 3 times higher than of cubs whose mothers died (0.14, 95% CI =

0.03−0.34); Table 10). With sex additive to mother status, survival estimates of male and female cubs (0.54, 0.49, respectively) with living mothers were 3 to 4 times higher than for cubs of those sexes (0.16, 0.12, respectively) with mothers that died. With period additive to mother status, survival estimates of cubs with living mothers in the reference (0.53) and the treatment (0.49) periods were over 3 times higher than of cubs with mothers that died in the reference (0.16) and treatment (0.13) periods. With sex interacting with period and additive to mother status in the reference period, survival estimates of male (0.74) and female (0.37) cubs with living mothers were 2 to 7 times higher than for cubs of those sexes (0.38, 0.05, respectively) with mothers that died. In the treatment period, survival estimates of male (0.44) and female (0.59) cubs with living mothers were 3 to 6 times higher than for cubs of those sexes (0.08, 0.19, respectively) with mothers that died. Period alone ranked relatively low as a covariate explaining variation in cub survival ($\Delta QAIC_c$ = 5.8; Reference period cub $\hat{S}$ = 0.50, 95% CI = 0.28−0.69; Treatment period cub $\hat{S}$ = 0.34, 95% CI = 0.18−0.51).

The survival of mothers during the time that cubs were dependent was vital to cub survival. © CPW PHOTO BY KEN LOGAN.

Table 9. Top ranking survival models with <2 ΔAIC_c units for adult and subadult pumas, and estimated adult annual and subadult stage survival rates with 95% Confidence Intervals (CI), 2005−2014, Uncompahgre Plateau, Colorado, USA.

Life stage	Model	Sex	Reference period survival (95% CI)	Treatment period survival (95% CI)
Adult[a]	Sex × Period	Male	0.96 (0.75−0.99)	0.40 (0.22−0.57)
		Female	0.86 (0.72−0.94)	0.74 (0.63−0.82)
	M × Period (F constant)	Male	0.96 (0.75−0.99)	0.40 (0.22−0.57)
		Female	0.78 (0.70−0.85)	
Subadult[b]	M × Period (F constant)	Male	0.92 (0.57−0.99)	0.43 (0.25−0.60)
		Female	0.68 (0.43−0.84)	
	Sex × Period	Male	0.92 (0.57−0.99)	0.43 (0.25−0.60)
		Female	0.63 (0.17−0.89)	0.70 (0.39−0.88)

[a]Sample sizes of adult pumas included 11 males, 21 females in the reference period and 22 males, 39 females in the treatment period.
[b]Sample sizes of subadult pumas included 14 males, 8 females in the reference period and 34 males, 19 females in the treatment period.

Table 10. Top ranking survival models with <2 $\Delta QAIC_c$ units for puma cubs monitored in the reference (27 males, 28 females) and treatment (36 males, 27 females) periods, and the estimated survival rates with 95% Confidence Intervals (CI), 2005−2014, Uncompahgre Plateau, Colorado, USA.

Model	Covariates		Survival (95% CI)
MotherId	Mother alive		0.51 (0.35−0.66)
	Mother dead		0.14 (0.03−0.34)
Sex + MotherId	Male	Mother alive	0.54 (0.33−0.71)
	Female	Mother alive	0.49 (0.27−0.67)
	Male	Mother dead	0.16 (0.03−0.41)
	Female	Mother dead	0.12 (0.02−0.34)
Period + MotherId	Reference	Mother alive	0.53 (0.31−0.71)
	Treatment	Mother alive	0.49 (0.27−0.69)
	Reference	Mother dead	0.16 (0.01−0.49)
	Treatment	Mother dead	0.13 (0.03−0.33)
Sex × Period + MotherId	Male, Reference	Mother alive	0.74 (0.37−0.92)
	Female, Reference	Mother alive	0.37 (0.14−0.62)
	Male, Reference	Mother dead	0.38 (0.03−0.79)
	Female, Reference	Mother dead	0.05 (0.00−0.33)
	Male, Treatment	Mother alive	0.44 (0.19−0.68)
	Female, Treatment	Mother alive	0.59 (0.27−0.82)
	Male, Treatment	Mother dead	0.08 (0.01−0.30)
	Female, Treatment	Mother dead	0.19 (0.03−0.47)

Puma reproduction

Adult female pumas on the UPSA produced litters in the months of March to September. Data on 66 birth dates revealed that births increased rapidly in May and June, peaked in July, declined slightly in August and rapidly declined in September. No live births were detected from October through February (Fig. 12).

■ Litters conceived ■ Litters born
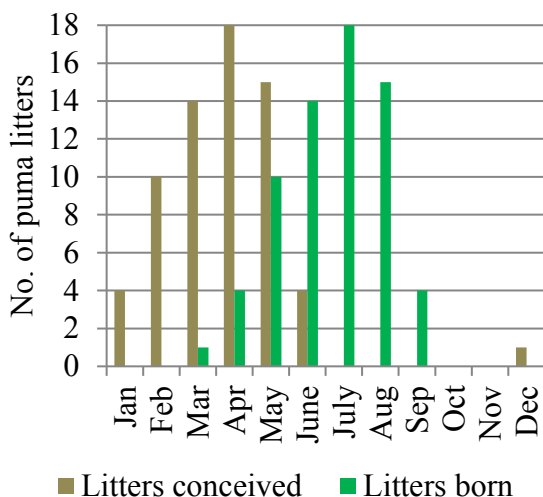
Figure 12. Monthly puma conception and birth frequency from May 19, 2005 to September 30, 2014 (n = 66 litters of 33 females); 60 litters were examined at nurseries when cubs were 25−45 days old, 4 litters were confirmed by tracks of ≥1 cubs following GPS- and VHF-collared mothers and 2 litters by remains of cubs of 2 GPS-collared mothers when cubs were ≤45 days old, Uncompahgre Plateau, Colorado, USA.

We estimated gestation for 17 litters by 13 females that produced minimum and maximum estimates. Gestation length medians were 91_{min}−92_{max} days and averages were 90.4_{min}−91.8_{max} days (95% CI_{min} = 89.1−91.6; 95% CI_{max} = 90.8−92.9). Considering an average 92-day gestation period and the distribution of birth months on the UPSA, puma breeding activity spanned the months of December to June, increased in February, and peaked March through May when 71% of the litters were conceived (Fig. 12).

The estimated average age that 14 females (12 approximately aged by our methods, 2 of known age) gave birth to their first litters was 32 months (95% CI = 27−36, range 21−48). Those females conceived at the average age of 29 months (95% CI = 24−33, range 18−45) assuming an average 92-day gestation period.

Reproduction parameter estimates, including average birth interval length, average litter size, proportions of male and female nurslings, and parturition rate in the reference and treatment periods were similar (Table 11). The 95% CIs on the differences of the estimates for each period for all tests included zero.

Puma hunters

The number of hunters requesting a permit to hunt on the UPSA each hunting season in the treatment period ranged from 66−78 (Table 12). The number of hunters that responded to the voluntary surveys in the 5 seasons ranged from 40−62, representing 56−79% of hunters that requested permits. Hunters did not answer all the questions on the survey, especially if they did not harvest a puma. The estimated number of active hunters on the UPSA each season ranged from 38−54. The highest numbers of hunters participated during TY1−TY3 when the quota was 8 pumas, with the highest number in TY1. The lowest numbers of hunters were in TY4 and TY5 when the quota was 5 pumas. Hunters on the UPSA generally used dogs to hunt pumas, yet 1−4 hunters (median = 4) each winter said they did not use dogs. Forty-nine of 52 hunters indicated on their surveys that presence of marks (i.e., collar, eartags) would not influence their decision to harvest a puma. Two hunters indicated marks would make them more likely to harvest a puma; 1 killed a marked adult male and 1 killed a non-marked adult female. One hunter reported he would be less likely to harvest a marked puma; this hunter treed and released 2 different marked adult females and did not kill any others.

Table 11. Puma reproduction parameter estimates and 95% Confidence Intervals (CI) in the reference and treatment periods, 2005−2014, Uncompahgre Plateau, Colorado, USA.

Reproduction parameter (units)	Period	Sample size	Estimates (95% CI)	95% CI on the difference[a]
Average birth interval (months)	Reference	17 intervals, 10 mothers	18.3 (15.5−21.1)	−3.1−5.4
	Treatment	13 intervals, 10 mothers	19.4 (16.2−22.6)	
Average litter size (cubs/litter)	Reference	26 litters, 14 mothers	2.8 (2.4−3.1)	−0.1−0.9
	Treatment	21 litters, 14 mothers	2.4 (2.0−2.8)	
Proportions of the sexes in litters (males, females)	Reference	41 male, 31 female	0.57 (0.45−0.69), 0.43 (0.31−0.55)	−0.023−0.301
	Treatment	27 male, 22 female	0.55 (0.40−0.69), 0.45 (0.31−0.60)	−0.101−0.305
	Both periods	68 male, 53 female	0.56 (0.47−0.65), 0.44 (0.35−0.53)	0.000−0.248
Average parturition rate (proportion of adult females/year)	Reference	12−13 adult females/year	0.63 (0.49−0.75)	−0.12−1.32[b]
	Treatment	13−17 adult females/year	0.48 (0.37−0.59)	

[a]Inferences on period effects on these parameters was made by examining the 95% CIs on the differences of the estimates for each period using the delta method (Seber 1982). The 95% CIs on the differences for all tests included zero.
[b]This 95% CI for the difference on the estimates is on the logit scale.

Table 12. Puma hunter participation during treatment year 1 (TY1) to treatment year 5 (TY5), 2009−2014, Uncompahgre Plateau Study Area (UPSA), Colorado, USA.[a]

Treatment year	No. hunters requested permit	No. hunters responded to survey	% of hunters that returned survey	No. hunters indicated hunted on UPSA	Estimated No. hunters that hunted on UPSA
TY1	78	62	79	43	54
TY2	70	50	71	31	43
TY3	73	40	56	28	51
TY4	70	43	61	24	39
TY5	66	45	68	26	38

[a]Puma hunting quotas on the UPSA included 8 pumas during TY1−TY3 and 5 pumas during TY4 and TY5.

Harvest quotas on the UPSA during TY1−TY5 were reached by 11 December to 10 January each winter; the median date was 23 December. Only hunters using dogs harvested pumas. The number of days that hunters took to reach the 8 puma quota during TY1−TY3 ranged from 21−33 (Table 13). To reach the 5 puma quota in TY4 and TY5, it took 41 and 54 days, respectively. The number of days that each hunter hunted on UPSA ranged from 1−14, with medians of 1−2. Hunter effort to harvest a puma ranged from 1−6 days, with medians of 1−2 days. During TY1−TY3 the number of days that hunters took to harvest a puma ranged from 1−4 (median = 1). It typically took the same number of days to harvest a male or female puma (median = 1), but the range was larger for males (1−4 days) than for females (1−2 days). During TY4 and TY5 the number of days to harvest a puma ranged from 1−6 (median = 1.5). The number of days hunted to harvest a female puma ranged from 1−3 (median = 1), whereas days to harvest a male ranged from 1−6 (median = 2).

Hunters reported they encountered more fresh tracks (i.e., <1 day old) of female pumas than of males during TY2, TY3, and TY5 (the survey in TY1 did not address this question), with annual male: female ratios ranging from 1:1.5−1:2.2 (Table 14).

But, in TY4 hunters reported they encountered more fresh tracks of males than females by a ratio of 1.8:1. The ratio of male to female tracks encountered by hunters in TY2, TY3, and TY5 reflected the observed male to female ratio of independent pumas in the population TY1−TY5, which annually ranged from 1:1.2−1:2.8. Our researchers encountered more fresh tracks of females than males each treatment year during our post-hunting capture operations, consistent with the sex structure of the independent pumas in the population after the hunting seasons.

Hunters self-identified as a selective hunter 84−97% of the time and the sex ratio of independent pumas killed by hunters (2.2 males:1 female) reflected selection toward male pumas (Table 14). Hunters harvested more male than female pumas, even though hunters reported encountering more fresh female tracks in 3 of 4 seasons when this survey question was asked. Puma hunters reported capturing and releasing 7 male and 19 female independent pumas during TY1−TY3. But in TY4 and TY5 hunters reported they caught and released 1 and 3 independent males, respectively, and 0 independent females.

Table 13. Lincoln-Petersen estimates ($\hat{N}_c$) of independent puma abundance and puma hunting and hunter survey results during treatment year 1 (TY1) to treatment year 5 (TY5), 2009−2014, Uncompahgre Plateau Study Area (UPSA), Colorado, USA.

Treatment year	$\hat{N}_c$	Harvest quota	Actual harvest	No. days hunted on UPSA (range, median, n)	No. days to fill the quota	No. days per successful hunter to kill a puma (range, median)
TY1	57	8	9	1−14, 2, 51	26	1−4, 1
TY2	56	8	8	1−12, 2, 35	21	1−3, 1.5
TY3	44	8	8	1−6, 1, 31	33	1−3, 1
TY4	43	5	5	1−12, 2, 23	41	1−6, 1
TY5	37	5	5	1−5, 2, 32	54	1−5, 2

Table 14. Counts arranged by sex ratio (M:F) of puma tracks, pumas harvested, pumas captured and released by hunters, puma tracks by researchers, and of independent pumas counted for Lincoln-Petersen (LP) estimates, and ratio of hunters that self-identified as selective:non-selective hunters, treatment year 1 (TY1) to treatment year 5 (TY5), 2009−2014, Uncompahgre Plateau Study Area, Colorado, USA.

Treatment year	Sex ratio of 1st puma tracks <1 day old encountered by hunters[a]	Sex ratio of hunter-killed pumas	Sex ratio of pumas caught and released by hunters	Ratio of hunters that self-identified as selective:non-selective	Sex Ratio of 1st puma tracks <1 day old encountered by researchers	Sex ratio of independent pumas counted for LP estimates pre-harvest	Sex ratio of independent pumas counted for LP estimates post-harvest
TY1	NA[b]	6:3	5:9	23:1	NA[b]	26:27	20:24
TY2	10:20	6:2	1:7	30:1	21:47	21:32	15:30
TY3	6:13	5:3	1:3	22:2	12:70	17:25	12:22
TY4	13:7	3:2	1:0	21:4	23:46	11:29	8:27
TY5	8:12	4:1	3:0	23:2	11:37	13:22	9:21

[a]Tracks were assumed to be of independent pumas.
[b]NA (Not addressed in hunter survey in TY1).

Chapter 5. Discussion

Overarching demographic effects of hunting

We found that annual harvest rates averaging 22% of marked independent pumas at the larger population-scale and 15% of the estimated number of independent pumas on the UPSA-scale over 4 years resulted in a 35% decline in abundance of independent pumas using the UPSA. As noted previously, however, the 15% UPSA-scale average harvest rate is biased. Hunting deaths were largely additive as indicated by a decline in survival and abundance, with no reduction in other causes of mortality, and hunting mortality that was not fully compensated by reproduction and recruitment. Recruitment of young pumas did not compensate for losses of adult males, but partially compensated for losses of adult females. The decline in puma abundance on the UPSA was likely due to the higher harvest rates occurring at the population-scale that included independent pumas on the UPSA, those with home ranges overlapping the UPSA, and animals on adjacent management units. We found that puma hunters exhibited selection for male pumas, which reduced male survival and affected the sex and age structure of the population.

Change in puma abundance

Abundance of independent pumas changed on the UPSA as we manipulated hunting. Puma abundance increased with the absence of hunting on the UPSA and protection of marked pumas from hunting in adjacent management units. This occurred even with other natural and human causes of mortality acting on the pumas. Thus, hunting mortality as it was applied prior to our study probably had reduced the abundance of pumas on the UPSA to a low phase and well below the capacity of the habitat. Moreover, the high finite growth rates of independent pumas on the UPSA, especially during RY4−RY5 and RY5−TY1 (i.e., λ = 1.25 and 1.39, respectively), suggested that if the population continued to be protected from hunting, the abundance of

independent pumas would likely have increased further. Theoretically, had the non-hunted puma population been naturally limited by food and regulated by competition, population growth would have declined (Logan 2019, Ruth et al. 2019). The decline, however, could follow a 4−8 year time lag (Laundre et al. 2007, Pierce et al. 2012). In our study, though, the absence and presence of hunting mortality determined population growth within the extents of the reference and treatment periods.

Our findings along with those from other western states reveal the range of puma population responses to variations in harvest rates (Fig. 13). At one end of the spectrum, a study in Utah revealed that abundance of independent pumas in the Monroe Mountains declined by more than one-half when subjected to an average 10% harvest rate (range 7−12) over 6 years. That same population subsequently increased close to previous abundance when subject to an average harvest rate of 5% (range 4−9) over 10 years (Wolfe et al. 2016). At the other extreme, pre-hunt estimates of independent pumas in a Wyoming population declined by 41% after 2 years with annual harvests rates of 43% and 44%. When harvest rates were reduced to an average 18% (range 14−23) the next 3 years the population increased to previous abundance by spring of the third year (Anderson and Lindzey 2005). The Wyoming study reports the highest known average harvest rate (i.e., 18%) associated with an increasing puma population. In this particular case, density-dependent population growth (*sensu* Logan and Sweanor 2001) might have regulated the rate of population recovery. In Washington, Beausoleil et al. (2016) estimated puma density and found population trend over 9 years to be stable or declining with an average annual harvest rate of 14% (range 7−21) of independent pumas.

Caution is warranted in interpreting results from these cases just as we noted biases with our own LP abundance estimates and the derived harvest rates on the UPSA. Potential biases in reported puma population sizes and harvest rates should be considered when minimum puma abundance indices are used (Wolfe et al. 2016) and

abundance estimation methods require an assumption of population closure (Anderson and Lindzey 2005, Beausoleil et al. 2016) unless convincing evidence on geographic and demographic closure are provided to support the assumption. Moreover, reported variations in effects of hunting mortality on puma abundance may partly be due to the population segment scales used in harvest rate estimation and variations in capacities for puma population growth, including: puma density relative to ecological carrying capacity, regional puma population demographics, other competing carnivores, and other management actions.
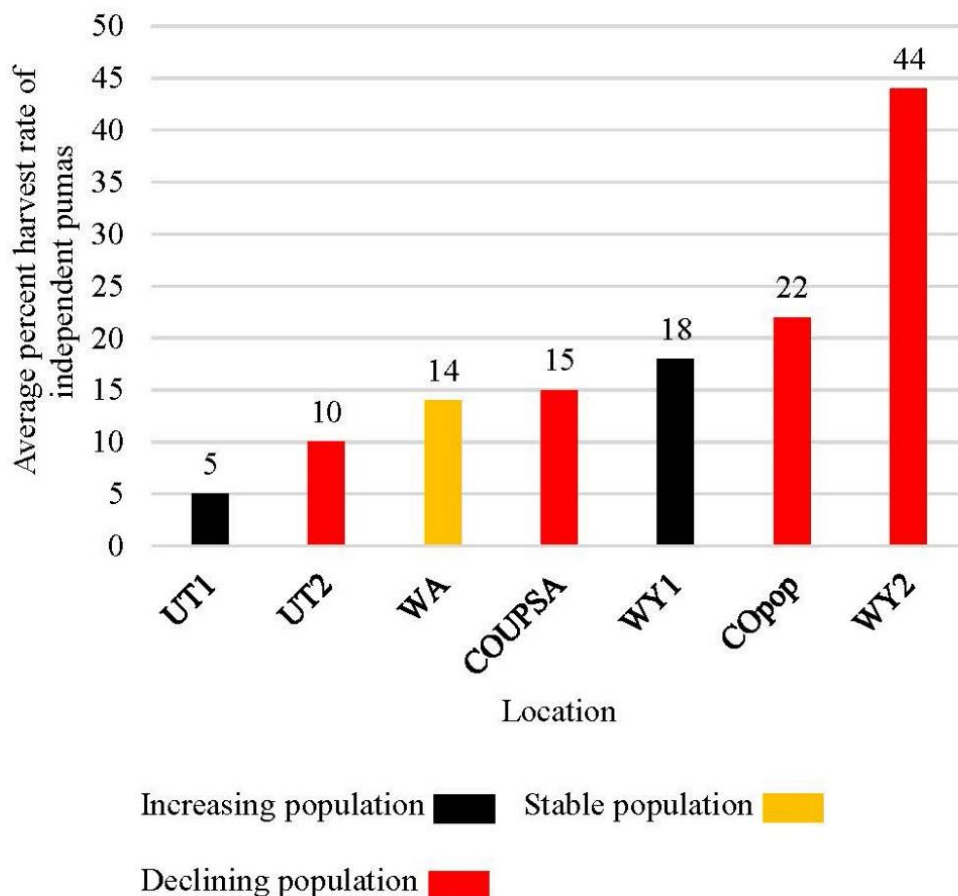
Figure 13. Average percent harvest rates of independent pumas associated with population trends reported in North America. Location designations refer to UT1 and UT2 (Utah, Wolfe et al. 2016), WA (Washington, Beausoleil et al. 2016), COUPSA (this study biased UPSA-scale average harvest rate), COpop (this study average population-scale harvest rate), WY1 and WY2 (Wyoming, Anderson and Lindzey 2005).

Consistent with other research, we found that 21% and 23% of adult females in the total harvest at the population-scale and the UPSA-scale, respectively, was associated with the decline in abundance of independent pumas that used the UPSA and surrounding area. The Wyoming puma population declined when adult females comprised about 25% of the harvest, but sustained a harvest comprised of 10−15% adult females (Anderson and Lindzey 2005). Researchers in southern Idaho and northern Utah suggested that a harvest that included 15−20% adult females probably would not reduce a puma population (Laundré et al. 2007).

Puma mortality and survival

In the absence of hunting on the UPSA adult pumas died primarily of natural causes, and human-caused deaths were rare. Deaths of subadults that occurred on the UPSA, by any cause, were unusual. Survival rates of adult and subadult males were high and exceeded those of their female counterparts. In contrast, regulated hunting in the treatment period reduced the survival of adult females, males, and subadult males. Survival of independent males was substantially lower than of the independent females. Because of the ranging behavior of independent pumas, especially males, some pumas were subject to hunting mortality on the UPSA and adjacent areas, which increased the risk of hunting mortality to those animals beyond the harvest limits set on the UPSA.

At the puma population levels and harvest rates in our study there was no compensation of hunting-caused mortality by a reduction in frequency of other causes of death for marked independent pumas in the treatment period. Natural mortality rates varied, and averaged about the same in the reference and treatment periods. But, total mortality in the treatment period increased by 3−7 times over that in the reference period, primarily from hunting. Moreover, abundances of adult and independent pumas declined with the addition of hunting.

Hunting-caused deaths added to other mortality in other puma populations in North America. Researchers in Utah (Lindzey et al. 1992), Wyoming (Anderson and Lindzey 2005), and Montana (Robinson and DeSimone 2011) found that puma populations declined or increased as hunting mortality rates were increased or reduced, characteristics of additive mortality from hunting. Furthermore, researchers in Washington (Cooley et al. 2009*a*) and Montana (Robinson et al. 2014) directly addressed this issue and concluded that hunting mortality was additive at the puma population and harvest levels they studied. In Utah, Wolfe et al. (2015) could not reject the additive mortality hypothesis of hunting for a heavily harvested puma population. They detected partial compensation of hunting mortality, however, associated with a decline in natural mortality in a lightly hunted puma population. To our knowledge the extent to which hunting mortality is additive or

compensatory in puma populations that have reached or exceeded ecological carrying capacity (*sensu* Fryxell et al. 2014) has not been investigated. There may also be an extra-additive mortality effect (Creel and Rotella 2010) operating at increased levels of female harvest. When mothers with litters die, the cubs will likely die (as in our study) and reduce potential recruitment to the population.

Hunting mortality added to mortality from other causes. © CPW PHOTO BY KEN LOGAN.

Adult males on the UPSA were the most affected by hunting, due to hunter selection, resulting in >50% decline in annual survival, a 59% decline in winter abundance, an almost halving in abundance of adult males <6 years old, and likely elimination of males >6 years old, all within 4 years. These demographic changes might alter the puma breeding process. Pumas have a polygamous and promiscuous mating system (Seidensticker et al. 1973, Anderson 1983, Logan and Sweanor 2010). Studies of non-hunted puma populations show that multiple territorial males compete for access to mates, and adult females choose mates from multiple available adult males and exhibit reproductive fidelity to males they chose in previous breeding seasons. Adult males in the same population exhibit highly variable individual reproductive success with a few adult males, especially the oldest, exhibiting the highest success (Murphy 1998, Logan and Sweanor 2001). This process is expected to favor the fittest males (Darwin 1859, Andersson 1982, Jones and Ratterman 2009). Moreover, long-lived territorial adult males may establish tolerant if not amicable relationships (beyond breeding) with adult females residing in their

territories that contribute to the fitness of the participating animals via higher survival of the adults and their offspring (Logan and Sweanor 2001, Ruth et al. 2011, Elbroch et al. 2017). Such a condition resulting in mating competition, mate selection, and social relationships likely occurred on the UPSA where after 5 years of no hunting the abundance of adult males approached that of adult females and adult survival was high. Also, the long period of dependence for puma young reduces the operational sex ratio (i.e., the ratio of reproductively receptive males to receptive females; Clutton-Brock 2007), favoring adult males and is expected to intensify mating competition (Logan and Sweanor 2001). In hunted puma populations with high adult male turnover, however, mating is expected to be constrained to relatively few available younger adult males with each male having low reproductive success (Logan and Sweanor 2010). For instance, in a Montana puma population reduced by hunting, 60% of litters were sired by males 30−37 months old (Onorato et al. 2011), and the oldest male was 6 years old (Robinson and DeSimone 2011). Thus, sexual selection processes may be relaxed (Mysterud 2011). This outcome was plausible on the UPSA when pumas were hunted, with all harvest occurring November to January and 92% of all litters sired afterwards, February through June. It is unknown if altering the breeding process through hunting-induced demographic changes affects the long-term fitness of pumas. To address this question, long-term research is needed on non-hunted and hunted puma populations where demographics, breeding behavior, survival, and individual reproductive success are studied (e.g., Milner et al. 2007, Bischof et al. 2018, Newbolt et al. 2017, Van de Kerk 2019).

Growth in hunted puma populations has been shown to be most sensitive to adult female survival (Martorello and Beausoleil 2003, Lambert et al. 2006, Robinson et al. 2014). Empirical evidence on adult female survival rates and population growth in western North America reveal that puma populations have a greater tendency to decline when annual adult female survival is ≤0.78 (Fig. 14, **Appendix IV**). An exception is a puma population in competition with wolves on the Greater Yellowstone Northern Range that declined with an adult female annual survival rate of 0.84 (Ruth et al. 2011, 2019). Puma populations have a greater tendency to increase when adult female annual survival rates are ≥0.86.

Adult female survival drives puma population growth and resilience to hunting mortality.
© CPW PHOTO BY KEN LOGAN.
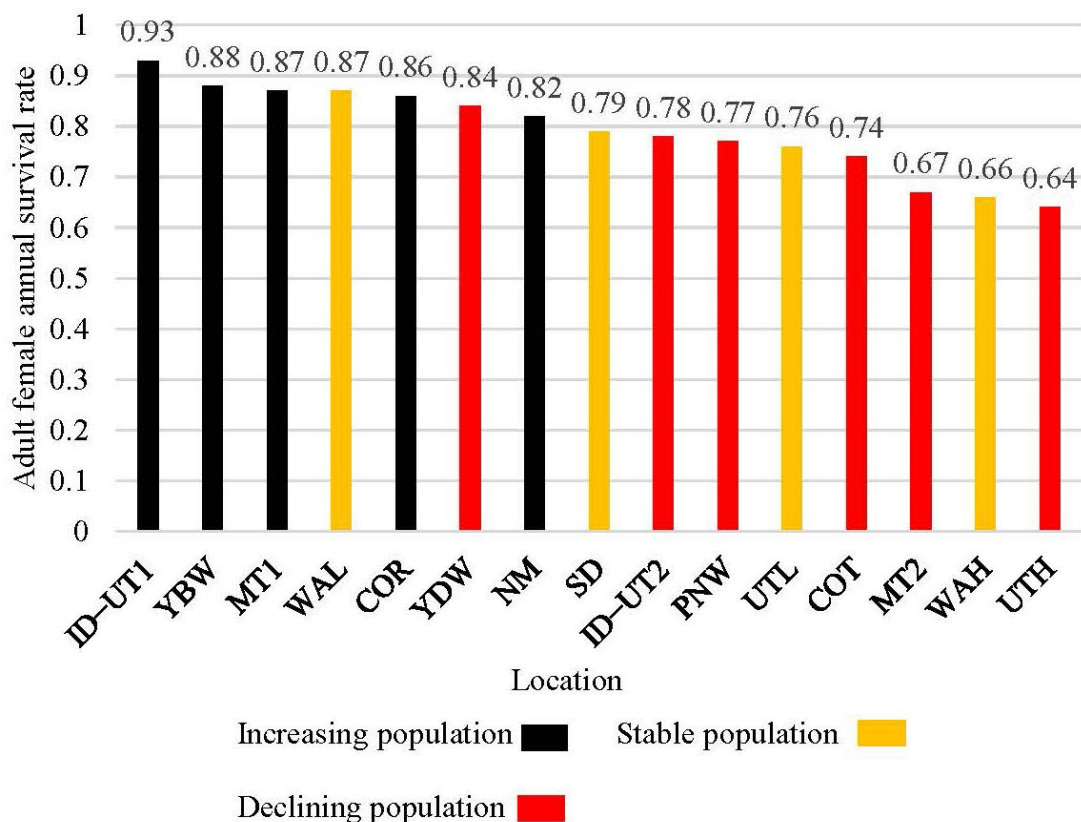
Figure 14. Adult female puma annual survival rates associated with population trends in North America. Location designations refer to ID−UT1 and ID−UT2 (Idaho and Utah, Laundré et al. 2007), YBW and YDW (Greater Yellowstone Northern Range before and during occupation by wolves, respectively; Ruth et al. 2011, 2019), MT1 and MT2 (Montana, Robinson and Desimone 2011), WAL and WAH (Washington low and high harvest, respectively, Cooley et al. 2009*a*), COR and COT (this study reference period and treatment period, respectively), NM (New Mexico, Logan and Sweanor 2001), SD (South Dakota, Jansen 2011), PNW (Pacific Northwest, Lambert et al. 2006), UTL and UTH (Utah low and high harvest, respectively, Stoner et al. 2006).

Moreover, the risk of losing adult females to hunting is important because in any year females rearing dependent young may comprise a majority of the adult females in the population, a phenomenon in our study and in puma populations in New Mexico, Washington, and Montana (Logan and Sweanor 2001, Cooley et al. 2009*b*, Robinson et al. 2014, respectively). Adult females in our study were not affected as much by hunting as were adult males due to hunters' preferences to harvest males. Nevertheless, the survival of mothers while cubs were dependent was vital to cub survival. Similarly, in Montana, Robinson and DeSimone (2011) found that hunting influenced cub survival mainly due to the deaths of mothers.

Cub survival estimates on the UPSA were generally lower than in 5 of 7 other western states, and was most similar to cub survival in the Greater Yellowstone Northern Range (Ruth et al. 2011; **Appendix IV**). In that population, which was lightly hunted and subject to competition with wolves and grizzly bears, Ruth et al. (2011) found that cub survival increased

with elk calf biomass. We did not have data specific to the UPSA to test if cub survival varied with prey abundance. All starvation we observed in cubs occurred because their mothers were not alive to provision them. Cubs in a heavily hunted population in Washington had the lowest survival (Cooley et al. 2009*a*). Variation in reported cub survival estimates among the studies, however, may be affected by the ages of cubs included in the respective analyses. Inclusion of nurslings tends to result in lower survival estimates than data skewed toward older cubs as the majority of mortality occurs in cubs ≤5 months old (this study, Logan and Sweanor 2001, Jansen 2011, Ruth et al. 2011).

Infanticide occurred at high frequencies on the UPSA in both periods. Infanticide was primarily associated with male pumas and tended to be higher in the reference period with an increasing abundance of adult males than in the treatment period with a declining abundance of adult males. Though, this did not lead to an increase in cub survival in the treatment period, likely due to concurrent increases in mortality of attending mothers. Ruth et al. (2011:1386) hypothesized "that instability of adult males, whether through removal (hunting or management related) or during reestablishment and population recovery, can result in increased [puma cub] mortality". Presumably this would occur as adult male pumas compete for access to mates (Hrdy 1979, Logan and Sweanor 2010). The theory holds that periods of male territory instability reduce cub survival via increased infanticide as immigrant males and shifting adult males move into vacated territories and compete for mates (Logan and Sweanor 2001, Ruth et al. 2011). Our results indicated that infanticide certainly occurred in both conditions as hypothesized by Ruth et al. (2011), and contributed to relatively low cub survival on the UPSA. We could not test if infanticide rates declined with adult male puma territorial stability, however, because adult male territoriality was unstable in both the reference and treatment periods.

Puma reproduction

There were few differences in birth interval length, litter size, proportion of males and females in litters, and parturition rates between the reference and treatment periods. Thus, there was no evidence of a compensatory reproduction response associated with hunting mortality.

Furthermore, there is no evidence that pumas in North America increase reproduction to compensate for hunting mortality (**Appendix V**). Data from our study and from South Dakota (Jansen 2011) and Montana (Robinson et al. 2014) found litter sizes were similar in non-hunted and hunted conditions. Likewise, Cooley et al. (2009*a*) found that litter sizes did not differ in lightly hunted and heavily hunted study areas in Washington. Sex ratios of nurslings did not differ in non-hunted and hunted conditions on the UPSA, but they did in South Dakota, favoring males (Jansen 2011). The author of that study cautioned, however, that the results were likely an artifact of low sample size during a non-hunting period compared to the hunting period (*n* = 6, 25 litters, respectively). Just as we found on the UPSA in the non-hunted and hunted conditions, researchers in New Mexico found similar parturition rates in a non-hunted area and where the number of adult pumas were experimentally reduced by one-half (Logan and Sweanor 2001). Both in Washington (Cooley et al. 2009*a*) and Montana (Robinson et al. 2014), mean maternity rates (i.e., no. kittens/adult female/yr) did not differ between lightly hunted and heavily hunted, or hunted and non-hunted populations, respectively.

There is no evidence that pumas in North America compensate for hunting mortality by increasing reproduction. © CPW PHOTO BY KEN LOGAN.

The timing of observed puma births in North America may be influenced by weather conditions interacting with variations in prey

abundance and distribution that affect cub survival. Cubs born during spring to fall are expected to have advantages for survival because of moderated weather conditions and increasing abundance and diversity of vulnerable prey (Laundré and Hernández 2007, Jansen and Jenks 2012). Alternatively, cubs born in winter are expected to have lower survival and die as nurslings (Laundré and Hernández 2007). We could not test hypotheses about seasonal variation in cub survival, however, because we did not observe any births from October through February. Also as a practical matter, early neonate deaths are expected to exacerbate the ability of researchers to detect such births (Logan and Sweanor 2001). Our observations of births on the UPSA primarily in early spring and summer (i.e., May to August) and peaking June to August were similar to birth distributions in South Dakota and Wyoming (Jansen and Jenks 2012, Elbroch et al. 2015, respectively). Puma births in Utah and Idaho (Laundre and Hernandez 2007) and in Montana (Robinson and DeSimone 2011) occurred almost year-round, but peaked July to October. In the Greater Yellowstone Northern Range, almost all births occurred from April to November with a major peak May to July and a second minor peak August to October (Ruth et al. 2019). In southern New Mexico, however, puma litters occurred almost year-round with a high frequency of births extending from May to October with a peak from July to September (Logan and Sweanor 2001). Some births that occur outside of the peak periods can be explained by the fact that adult female pumas are polyestrous (i.e., cycle into reproductive receptivity continually until pregnant) and some mothers may lose entire litters at any time. Such females can resume estrous within as few as 1−3 weeks and usually in 3−4 months (Logan and Sweanor 2001, Ruth et al. 2019).

Puma recruitment

Puma population growth on the UPSA was affected by recruitment of both young female and male pumas from *in situ* reproduction and apparent immigration, and animals that emigrated. Offspring that exhibited philopatry as adults on the UPSA were infrequent, and mostly female. But, dispersal of young from natal areas was frequent, with some of these animals settling as adults in other parts of the UPSA.

Males emigrated more frequently and moved longer distances than females. Some pumas we captured as subadults with unknown origins were likely a combination of immigrants from elsewhere moving through or to the UPSA and non-marked offspring of mothers on the UPSA. We assumed some recruitment on the UPSA was from immigration, because we observed subadult pumas emigrating from the UPSA and expected other subadults were moving into the UPSA. Recruitment in the reference period resulted in an increasing abundance of adult pumas. In the treatment period, although there were more 1−2 year old animals (than in the reference period), recruitment was insufficient to replace losses of adult pumas, particularly males; but, it apparently partially compensated for adult female losses in 2 of 4 years (i.e., TY2 and TY4).

Philopatry and dispersal of young independent pumas have been reported by other researchers. Anderson et al. (1992) reported that pumas on the Uncompahgre Plateau in the 1980s also exhibited characteristics similar to our observations with philopatry exhibited by some females, although most females dispersed, and males dispersed more frequently and at longer distances than females. Investigators in New Mexico, the Northern Greater Yellowstone Ecosystem, and Utah reported that philopatry was usually exhibited by female pumas, that both female and male pumas dispersed, and males generally dispersed more frequently (Sweanor et al. 2000, Biek et al. 2006, Stoner et al. 2013, respectively). Longer dispersal distances were exhibited by males in New Mexico (Sweanor et al. 2000). But, there were no sex differences in dispersal distances reported in Utah, the Northern Greater Yellowstone Ecosystem, and the Blackfoot drainage in Montana (Stoner et al. 2013, Newby et al. 2013). Philopatric males apparently occur more frequently in Southern California and Florida where puma habitats are fragmented by human development to the extent of obstructing or constricting dispersal movements (Beier 1995, Maehr 1997, respectively). Dispersal by pumas, especially of males, is believed to be important in inbreeding avoidance and gene flow (Biek et al. 2006). Consequences of disrupted dispersal, as in California pumas, include lower genetic diversity and strong population genetic

structuring (Gustafson et al. 2019). Philopatry in male pumas living in connected habitat appears to be exceptional, with 2 cases reported in the Greater Yellowstone Northern Range (Ruth et al. 2019), and possibly 2 that we found. High adult male mortality, as we documented in our study, and the associated reduced male competition might favor young males expressing philopatry as an alternate strategy to dispersal, such as our 2 cases. Their deaths, though, from hunting at young ages might have precluded later dispersal.

The roles of emigration and immigration in puma population dynamics have been recognized in a number of regions in the western U.S., including New Mexico, Utah, Washington, the Greater Yellowstone Northern Range, the Great Basin, and Montana (Sweanor 2000, Stoner et al. 2006, Cooley et al. 2009*b*, Ruth et al. 2011, Andreasen et al. 2012, Robinson et al. 2014, respectively). These authors revealed that puma population segments interacted at a large landscape scale through immigration and emigration and recognized these as metapopulation processes (*sensu* Hastings and Harrison 1994) that along with *in situ* reproduction, mortality and recruitment determined population segment growth (Sweanor et al. 2000, Stoner et al. 2006, Cooley et al. 2009*b*, Newby et al. 2013). Our observations of pumas emigrating from the UPSA and their attendant long-distances moves to eastern Utah, northern New Mexico, and southern Wyoming indicated that pumas on the Uncompahgre Plateau are probably part of a larger metapopulation structure or one expansive contiguous population due to the connectedness of puma habitat in Colorado (McRae et al. 2005). In either case, local population segments or regions might exhibit varying growth rates influenced by the capacity of the environment and variable risks of mortality.

Puma population structure
Hunting mortality changed the puma population structure on the UPSA. The first 3 years of the reference period, with no hunting, indicated a puma population with very few pumas >6 years old, probably an effect of high hunting mortality prior to our study. With the continued absence of hunting, however, the age distribution increased as would be expected with the greater survival

of adults. After hunting resumed, the age distribution skewed younger, and abundance of adult males in particular declined, as expected with lower survival. Similar effects of hunting mortality on puma population age structure have been reported in New Mexico (Logan and Sweanor 2001), Wyoming (Anderson and Lindzey 2005), Utah (Stoner et al. 2006), Washington (Cooley et al. 2009*a*), and Montana (Robinson and DeSimone 2011).

The UPSA puma population in winter was structured similarly to other North America populations (Logan and Sweanor 2010). Adults represent multiple age cohorts and, thus, are the most abundant segment. Pumas have a polygynous, promiscuous mating system where adult females have smaller overlapping non-territorial home ranges compared to males and, thus, generally outnumber adult males which have large territories (Seidensticker et al. 1973, Logan and Sweanor 2001). Cubs, comprised about equally of males and females, are the second most abundant segment. This may be due to cub mortalities occurring prior to their first winter as a large majority of mortalities occur when cubs are ≤5 months old (this study, Logan and Sweanor 2001, Jansen 2011, Ruth et al. 2011).

The subadult segment, representing a single cohort, was the least abundant in winter on the UPSA. Other researchers that quantified population structure in winter in New Mexico (Logan and Sweanor 2001), Utah and Idaho (Laundre et al. 2007), and Montana (Robinson and DeSimone 2011) also found that subadults were the least abundant life stage. Studies in Alberta, New Mexico, Montana, and South Dakota indicated pumas averaged 15−16 months old at dispersal (Ross and Jalkotzy 1992, Sweanor et al. 2000, Laundre and Hernandez 2007, Robinson and DeSimone 2011, Jansen and Jenks 2012), similar to our observations. The average age of dispersal was 14 months in Wyoming (Anderson and Lindzey 2005). The low abundance of subadults we observed was probably partially due to mortalities that occurred in the cohort during the cub life stage, among subadults in the UPSA, and potential immigrating subadults outside the UPSA. For subadults, particularly males, mortality would be expected to be primarily from hunting (this

study, Newby et al. 2013). Furthermore, most subadults would be expected to emigrate from the UPSA before their first winter in the subadult stage, as demonstrated by UPSA subadults we monitored, and before our winter efforts to survey puma abundance. Likewise, a large majority of young pumas in the Snowy Range of Wyoming emigrated between the months of April and September (Anderson and Lindzey 2005). In Utah, Stoner et al. (2013) reported that subadult pumas emigrated primarily during March to June in association with heightened breeding behavior of adults.

Puma hunters

Puma hunters on the UPSA normally used dogs to catch pumas, which usually took refuge in trees. This enabled hunters to assess the sex of a captured puma prior to deciding to kill the animal. Abilities of hunters to distinguish puma sex may have been due to experience and to puma sex identification material provided to hunters through the CPW puma education and identification course made mandatory since 2007 (Colorado Parks and Wildlife 2017). Similarly, experienced puma hunters using dogs in Washington were able to correctly identify the sex of treed pumas 70% of the time (Beausoleil and Warheit 2015).

Hunters selected for male pumas even though they generally encountered fresh female puma tracks more frequently than male tracks and females were more abundant. Our researchers' observations of more fresh tracks of females than males were consistent with the hunters' reports. Hunters apparently encountered female tracks in relation to their relative abundance in the independent puma population. These results were contrary to the assumption that male pumas as a group are more vulnerable to hunting with dogs because hunters detect tracks of males more frequently than tracks of females (*sensu* Anderson and Lindzey 2005). Instead, it is more likely that males are more vulnerable due to selection by hunters using dogs. Hunters in Washington killed more male than female pumas when hunting with dogs, but more females than males when dogs were subsequently prohibited (Martorello and Beausoleil 2003). The authors explained this shift occurred because hunters with dogs could

practice selection, but when dogs were prohibited hunters encountered pumas by chance and killed the sexes relative to their abundance in the population. In Oregon, Clark et al. (2014:785) found that hunting pumas with dogs "greatly increased mortality of male [pumas] where male harvest was more than 2 times greater compared to when hunting with dogs was prohibited".

Hunters using dogs to capture pumas usually can determine the sex of the animals. © CPW PHOTO BY KEN LOGAN.

Puma hunter participation on the UPSA was highest when the harvest quota and puma abundance were high and lowest when the quota and puma abundance were low. Hunters used similar efforts to kill male and female pumas when pumas were relatively abundant, but they took longer to kill males when the abundance of adult males was low probably because hunters still preferred to practice selection. Similarly, hunters took more days to reach the quota when the quota and puma abundance were lowest probably because of a reduced chance of encountering independent pumas, especially preferred adult males.

Hunter selection resulted in demographic effects that included lower adult and subadult male survival and lower abundance and average age of independent males. Loss of adult territorial males may encourage the immigration of young males as they search for puma habitat with high prey availability, prospective mates, and reduced male competition (Logan and Sweanor 2001, Laundré and Hernández 2003, Robinson et al. 2008).

Chapter 6. Management Implications

Wildlife agencies can conserve and manage pumas by regulating hunting mortality. In our study, a harvest rate at the population-scale averaging 22% of independent pumas over 4 years and with >20% adult females in the total harvest greatly reduced puma abundance. Responses of puma populations to harvest vary across studies: harvest rates of independent pumas averaging 10% was associated with population decline in Utah (Wolfe et al. 2016), 14% with population stability or decline in Washington (Beausoleil et al. 2016), and 18% with population increase in Wyoming (Anderson and Lindzey 2005; Fig. 13). Our results followed an expected scale-dependent pattern in harvest rate estimates: as a focal area (e.g., for management or study) nears the size of a population, estimates become more accurate. The smaller the focal area relative to the area occupied by the puma population, the more that harvest rates will likely be underestimated.

Puma abundance is the basic parameter that managers must consider either empirically, or theoretically in harvest management. Prevalent in puma range are non-surveyed regions where managers routinely extrapolate demographic parameter estimates derived from the literature. Puma density assumptions in particular are commonly extrapolated to non-surveyed areas, have questionable accuracy, and are used to calculate proxies for puma abundance estimates for the setting of harvest limits. Errors in assumptions can thwart achievement of management objectives. Results from our study and others in North America indicate that reducing puma abundance with hunting, particularly with the use of dogs, is fairly easy to achieve. But, reliably managing puma population segments for conservation, while providing sustainable hunting opportunity, is more challenging. Thus, in non-surveyed areas managed for puma conservation and sustainable hunting, managers should apply conservative puma density assumptions and harvest rates to improve the odds of successful management. When resources allow for rigorous monitoring, puma abundance could be estimated over time

using newly developed genetic sampling and photographic mark-recapture methods in representative management units (e.g., Proffitt et al. 2015, Beausoleil et al. 2016, Alldredge et al. 2019). Concomitantly, relationships of puma abundance estimates to hunting data could be examined to develop indices to changes in puma abundance for other non-surveyed hunted areas (e.g., Anderson and Lindzey 2005, Wolfe et al. 2016).

Restricting human-caused mortality, especially from hunting, is fundamental to puma conservation. © CPW PHOTO BY KEN LOGAN.

Hunting is the only feature of puma mortality that managers can regulate to affect population size, as the other causes of mortality occur randomly and vary annually. Some non-hunting human causes of death (e.g., depredation control kills, some vehicle strikes) can be observed and quantified by managers, but natural deaths are rarely observed and some human-caused deaths (e.g., vehicle strikes, illegal killing) go unobserved. In addition, hunting deaths may not be compensated by increased puma survival, reproduction, and immigration (this study, Cooley et al. 2009*b*, Robinson et al. 2014, Wolfe et al. 2015). In areas managed to provide for puma conservation and sustained hunting opportunity and where total human-caused mortality metrics are used to set mortality limits, all detected human-caused mortalities of independent pumas occurring year-round could be counted in those limits. Hunted puma populations that were inadvertently reduced may recover to pre-decline abundance in as few as 3 years with harvest rates reduced by one-half or more (Anderson and Lindzey 2005). But it may take at least 3−5 years of total protection from

hunting for such populations to recover (this study, Logan and Sweanor 2001). In areas managed to reduce puma abundance, however, liberal removal of both sexes can achieve population reduction in 1−3 years (this study, Logan and Sweanor 2001, Anderson and Lindzey 2005, Lambert et al. 2006, Stoner et al. 2006, Robinson et al. 2014).

Pumas move across the landscape in ways that affect puma management. Regulated hunting used to manipulate puma abundance in smaller management units to address local issues (e.g., over-kill of adult female pumas, depredation on livestock) may be successful if managers recognize the effects of hunting pumas in those areas and adjacent areas. We demonstrated this in the reference period by protecting marked independent pumas in adjacent northern management units for 5 years, which contributed to high survival and increased abundance of independent pumas on the UPSA. Conversely, puma abundance declined when all independent pumas were legal game in the UPSA and surrounding management units. Moreover, the emigration of pumas from the UPSA to areas across southwest Colorado, eastern Utah, and as far as southern Wyoming and northern New Mexico suggested that the UPSA plausibly could be receiving immigrating pumas from just as far away. However, the emigration, dispersal distance, and establishment success of pumas could be negatively impacted by human-caused mortality, particularly from heavy harvest (Newby et al. 2013). This relationship of puma movements to management scale has long been recognized, "Because [pumas] disperse across management-unit boundaries, [puma] management prescriptions executed on one management unit could affect [puma] population dynamics on other units within [puma] dispersal range" (Sweanor et al. 2000:806; also see Anderson et al. 1992). Therefore, larger regions for puma management are more appropriate to the scale of puma movements and demographics. In our study system, that region ranged from about 11,600 to 12,300 km^2. The low range included the UPSA and 4 adjacent GMUs where marked pumas moved and prescribed our population-scale. The higher range included the UPSA and all 5 adjacent GMUs where the management objectives were

consistent (i.e., for a stable or increasing puma population state).

As we discussed previously, puma population segments respond in varied ways to hunting and metapopulation processes. Considering the fact that managers generally rely upon assumptions about puma demographics and effects of hunting in areas unless surveyed, they should consider the amounts of areas managed with objectives for population reduction relative to areas managed for stable or increasing abundance when puma conservation is a state-wide goal (Novaro et al. 2005). Associated with this concept, a source-sink management model has been recognized as a biologically valid approach for pumas in western North America that provides for puma conservation, hunting opportunity, options for mitigating puma-human and puma-wildlife conflicts, and a framework for research (Logan and Sweanor 2001, Laundré and Clark 2003, Stoner et al. 2006, Wyoming Game and Fish 2006, Robinson et al. 2008, Cooley et al. 2011, Newby et al. 2013, Robinson et al. 2014, Ruth et al. 2019). In a source-sink management structure hunting mortality is applied in a spatially variable manner and animals emigrate from protected or relatively lightly-hunted source population areas (i.e., recruitment exceeds death rates and the area is a net exporter of individuals) and are immigrants into more heavily hunted areas that act as sinks (i.e., death rates exceed recruitment) (Pulliam 1988, Hanski and Simberloff 1997, Runge et al. 2006, Stoner et al. 2013). Although there are some assumed protected (e.g., national parks and monuments, state parks) and lightly hunted areas, managers need to reckon the validity of those as sources by assessing the expected puma abundances within them, home range sizes, and movements in and around those areas and ascertain whether or not human-caused mortality along the perimeters might actually be creating sinks (Noss et al. 1996, Woodroffe and Ginsberg 1998, Ruth et al. 2011).

Selective hunters using dogs and trained in puma sex identification could influence puma demographics and facilitate puma source-sink management. Hunter selection can reduce hunting pressure on independent females and contribute to sustainable puma hunting. Selection by hunters for males, particularly

adults, can reduce independent male puma survival, reduce adult male abundance, and create a younger age structure. In addition, as puma abundance and the male component declines further, hunter selection or encounters with males could decline and is expected to result in higher adult female harvest (Anderson and Lindzey 2005), potentially with a reduction in survival of dependent cubs. Thus, protection of mothers and limits on adult female harvest are appropriate in areas managed for puma conservation and hunting. Similarly, in management plans where the roles of sex and age structure in puma life history strategies are deemed important for adaptive potential, conservative harvest rates and pursuit-only (i.e., with dogs) opportunities could be applied in an effort to maintain a natural population structure. Dispersal of non-selected pumas from hunted areas and refuges from harvest and into more heavily hunted areas with attendant recruitment and genetic mixing could counteract potential effects of selective harvest (Tenhumberg et al. 2004, Festa-Bianchet 2017). Conversely, hunters with dogs are capable of efficiently harvesting pumas and causing population declines in areas where that is a management objective.

Finally, managers could assess puma hunting as a management tool by examining relationships of response variables (e.g., ungulate survival rates, puma predation rates) to puma abundance or harvest data (e.g., Hurley et al. 2011). These efforts could be used in an adaptive management framework (Walters 1986, Williams et al. 2001) enabling managers to apply the best available information and practices to puma management (Cougar Management Guidelines Working Group 2005, Jenks 2011).

Puma management and conservation should be planned at large landscape scales to provide pumas essential requirements for survival, reproduction, movement, and inter-population processes. © CPW PHOTO BY KEN LOGAN.

Literature Cited

Alldredge, M. W., E. J. Bergman, C. J. Bishop, D. J. Freddy, and K. A. Logan. 2008. Pilot evaluation of predator-prey dynamics on the Uncompahgre Plateau. Federal Aid in Wildlife Restoration Report, Project W-185-R. Fort Collins, Colorado, USA.

Alldredge, M. W., T. Blecha, and J. H. Lewis. 2019. Less invasive monitoring of cougars in Colorado's Front Range. Wildlife Society Bulletin 43:222−230.

Amstrup, S. C., I. Stirling, and J. W. Lentfer. 1986. Past and present status of polar bears in Alaska. Wildlife Society Bulletin 14:241−254.

Anderson, A. E. 1983. A critical review of literature on puma *(Felis concolor)*. Special Report No. 54, Colorado Division of Wildlife, Ft. Collins, USA.

Anderson, A. E., D. C. Bowden, and D. M. Kattner. 1992. The puma on Uncompahgre Plateau, Colorado. Technical Publication No. 40, Colorado Division of Wildlife, Ft. Collins, USA.

Anderson, C. R., and F. G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildlife Society Bulletin 33:179−188.

Anderson, C. R., F. Lindzey, K. H. Knopff, M. G. Jalkotzy, and M. S. Boyce. 2010. Cougar management in North America, Pages 41−54 *in* Cougar: ecology & conservation, M. Hornocker and S. Negri, editors. University of Chicago Press, Chicago, Illinois, USA.

Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. Biological Journal of the Linnean Society 17:375−393.

Andreasen, A. M., K. M. Stewart, W. S. Longland, J. P. Beckmann, and M. L. Forister. 2012. Identification of source-sink dynamics in mountain lions of the Great Basin. Molecular Ecology 21:5689−5701.

Apker, J. 2005. Colorado mountain lion status report. Pages 57−64 *in* R. A. Beausoleil and D. A. Martorello, editors. Proceedings of the Eighth Mountain Lion Workshop, Olympia, Washington, USA.

Ashman, D.L., G. C. Christensen, M. L. Hess, G. K. Tsukamoto, and M. S. Wickersham. 1983. The mountain lion in Nevada. Final Report, Federal Aid in Wildlife Restoration Project W-48-15, Nevada Department of Wildlife, Reno, USA.

Barry, J. M., L. M. Ebroch, M. E. Aiello-Lammens, R. J. Sarno, L. Seelye, A. Kusler, H. B. Quigley, and M. M. Grigione. 2018. Pumas as ecosystem engineers: ungulate carcasses support beetle assemblages in the Greater Yellowstone Ecosystem. Oecologia. https://doi.org/10.1007/s00442-018-4315-z. Accessed 30 Nov 2018.

Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behavior in puma. Southwestern Naturalist 50:466−471.

Beausoleil, R. A., and K. I. Warheit. 2015. Using DNA to evaluate field identification of cougar sex by agency staff and hunters using dogs. Wildlife Society Bulletin 39:203−209.

Beausoleil, R. A., J. D. Clark, and B. T. Maletzke. 2016. A long-term evaluation of biopsy darts and DNA to estimate cougar density: an agency-citizen science

collaboration. Wildlife Society Bulletin 40:583−592.

Becker, S. A., D. D. Bjornlie, and D. S. Moody. 2003. Wyoming mountain lion status report. Pages 64−70 *in* S. A. Becker, D. D. Bjornlie, F. G. Lindzey, and D. S. Moody, editors. Proceedings of the Seventh Mountain Lion Workshop. Lander, Wyoming, USA.

Beier, P., D. Choate, and R. H. Barrett. 1995. Movement patterns of mountain lions during different behaviors. Journal of Mammalogy 76:1056−1070.

Beier, P. 2010. A focal species for conservation planning. Pages 177−189 *in* Cougar: ecology & conservation, M. Hornocker and S. Negri, editors. Chicago Press, Chicago, Illinois, USA.

Benson, J. F., J. A. Hostetler, D. P. Onorato, W. E. Johnson, M. E. Roelke, S. J. O'Brien, D. Jansen, and M. K. Oli. 2011. Intentional genetic introgression influences survival of adults and subadults in a small, inbred felid population. Journal of Animal Ecology 80:958−967.

Biek, R., N. Akamine, M. K. Schwartz, T. K. Ruth, K. M. Murphy, and M. Poss. 2006. Genetic consequences of sex-biased dispersal in a solitary carnivore: Yellowstone cougars. Biology Letters 2:312−315.

Bischof, R., C. Bonenfant, I. M. Rivrud, A. Zedrosser, A. Friebe, T. Coulson, A. Mysterud, and J. E. Swenson. 2018. Regulated hunting re-shapes the life history of brown bears. Nature Ecology & Evolution 2:116−123.

Bishop, C. J., G. C. White, and P. M. Lukacs. 2008. Evaluating dependence among mule deer siblings in fetal and neonatal survival analyses. Journal of Wildlife Management 72:1085−1093.

Brown, D. E., editor. 1984. The wolf in the Southwest: the making of an endangered species. The University of Arizona Press, Tucson, Arizona, USA.

Brown, E. E., and C. A. López Gonález. 2001. Borderland jaguars. The University of Utah Press, Salt Lake City, Utah, USA.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Cahalane, V. H. 1964. A preliminary study of distribution and numbers of cougar, grizzly and wolf in North America. New York Zoological Society, Bronx, New York, USA.

Casey, A. L., P. R. Krausman, W. W. Shaw, and H. G. Shaw. 2005. Knowledge of and attitudes toward mountain lions: a public survey of residents adjacent to Saguaro National Park, Arizona. Human Dimensions of Wildlife 10:29−38.

Clark, D. A., B. K. Johnson, D. H. Jackson, M. Henjum, S. L. Findholt, J. J. Akenson, and R. G. Anthony. 2014. Survival rates of cougars in Oregon from 1989 to 2011: A retrospective analysis. Journal of Wildlife Management 78:779−790.

Clark, D. A., B. K. Johnson, and D. H. Jackson. 2015. Monthly and annual survival rates of cougar kittens in Oregon. Northwest Science 89:393−400.

Clark, S. G., M. B. Rutherford, and D. J. Mattson. 2014. Large carnivores, people, and governance, Pages 1−28 *in* Large carnivore conservation: integrating science and policy in the North American West, S.

G. Clark and M. B. Rutherford, editors. Chicago Press, Chicago, Illinois, USA.

Clutton-Brock, T. 2007. Sexual selection in males and females. Science 318:1882−1885.

Colorado Parks and Wildlife. 2004. Colorado mountain lion management, data analysis unit review and revision, quota analysis and recommendation process. Denver, Colorado, USA.

Colorado Parks and Wildlife. 2017. Mountain lion education and identification course. http://www.cpw.state.co.us/Documents/Hunting/HunterEd/MountainLionEducationAndIdentificationCourse.pdf. Accessed 4 Feb 2018.

Cooch, E., and G. White. 2015. Program MARK: a gentle introduction. Fourteenth edition. Colorado State University, Fort Collins, USA.

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

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

Cooley, H. S., K. D. Bunell, D. C. Stoner, and M. L. Wolfe. 2011. Population management: Cougar hunting. Pages 111−133 *in* J. A. Jenks, editor. Managing cougars in North America. Jack H. Berryman Institute, Utah State University, Logan, USA.

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

Creel, S., and J. J. Rotella. 2010. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves *(Canis lupus)*. PLoS ONE 5(9): e12918. doi:10.1371/journal.pone.0012918.

Culver, M., W. E. Johnson, J. Pecon-Slattery, and S. J. O'Brien. 2000. Genomic ancestry of the American puma (*Puma concolor*). Journal of Heredity 91:186−197.

Darwin, C. 1859. On the origin of species by means of natural selection. J. Murray, London, United Kingdom.

Dawn, D. 2002. Management of cougars (*Puma concolor*) in the western United States. Thesis. San Jose State University, San Jose, California, USA.

Department of the Interior. 1973. Endangered Species Act. 1973: as amended through the 108th Congress. Department of the Interior, United States Fish and Wildlife Service, Washington, D. C., USA.

Elbroch, L. M., and H. U. Wittmer. 2012. Table scraps: inter-trophic food provisioning by pumas. Biology letters DOI:10.1098/rsbl.2012.0423. Accessed 19 June 2012.

Elbroch, L. M., P. E. Lendrum, P. Alexander, and H. Quigley. 2015. Cougar den site selection in the Southern Yellowstone Ecosystem. Mammal Research 60:89−96.

Elbroch, L. M., M. Levy, M. Lubell, H. Quigley, and A. Caragiulo. 2017. Adaptive social strategies in a solitary carnivore. Science

Advances. 3(10), e1701218 doi: 10.1126/sciadv.1701218.

Elbroch, L. M., L. Marescot, H. Quigley, D. Craighead, and H. U. Wittmer. 2018. Multiple anthropogenic interventions drive puma survival following wolf recovery in the Greater Yellowstone Ecosystem. Ecology and Evolution 8:7236−7245.

Festa-Bianchet, M. 2017. When does selective hunting select, how can we tell, and what can we do about it? Mammal Review 47:76−81.

Fryxell, J. M., A. R. E. Sinclair, and G. Caughley. 2014. Wildlife ecology, conservation, and management. Third edition. Wiley Blackwell, West Sussex, United Kingdom.

Gigliotti, L. M. 2005. Analysis of public opinions towards mountain lion management in South Dakota. Division of Wildlife Report. South Dakota Department of Game, Fish and Parks, Pierre, USA.

Gill, B. 2010. To save a mountain lion: evolving philosophy of nature and cougars. Pages 5−16 in M. Hornocker and S. Negri, editors. Cougar: ecology & conservation. University of Chicago Press, Illinois USA.

Goodman, L. A. 1965. On simultaneous confidence intervals for multinomial proportions. Technometrics 7:247−254.

Gustafson, K. D., R. B. Gagne, T. W. Vickers, S. P. D. Riley, C. C. Wilmers, V. C. Bleich, B. M. Pierce, M. Kenyon, T. L. Drazenovich, J. A. Sikich, W. M. Boyce, and H. B. Ernest. 2019. Genetick source−sink dynamics among naturally structured and anthropogenically fragmented puma populations. Conservation Genetics 20:215−227.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5−26 in I. A. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California, USA.

Hastings, A., and S. Harrison. 1994. Metapopulation dynamics and genetics. Annual Review of Ecology and Systematics 25:167−188.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21:5−39.

Hostetler, J. A., D. P. Onorato, J. D. Nichols, W. E. Johnson, M. E. Roelke, S. J. O'Brien, D. Jansen, and M. K. Oli. 2010. Genetic introgression and the survival of Florida panther kittens. Biological Conservation 143:2789−2796.

Hrdy, S. B. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethology and Sociobiology 1:13−40.

Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178:1−33.

Jansen, B. D. 2011. Anthropogenic factors affecting mountain lions in the Black Range Hills of South Dakota. Dissertation, South Dakota State University, Bismark, USA.

Jansen, B. D., and J. A. Jenks. 2012. Birth timing for mountain lions *(Puma concolor)*: testing the prey availability hypothesis. Plos

One 7(9): e44625. doi:10.1371/journal.pone.0044625.

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

Jones, A. G., and N. L. Ratterman. 2009. Mate choice and sexual selection: What have we learned since Darwin? Proceedings of the National Academy of Sciences 106:10001−10008.

Kellert, S. R., and J. K. Berry. 1987. Attitudes, knowledge, and behaviors toward wildlife affected by gender. Wildlife Society Bulletin 15:363−371.

Kellert, S. R., M. Black, C. R. Rush, and A. J. Bath. 1996. Human culture and large carnivore conservation in North America. Conservation Biology 10:977−990.

Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. Macleod, D. Paetkau, and G. C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. Journal of Wildlife Management 73:3−16.

Kreeger, T. J., J. M. Arnemo, and J. P. Raath. 1999. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals, Inc., Ft. Collins, CO, USA.

Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park Montana. Journal of Wildlife Management 63:901−910.

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.

Laundré, J. W., L. Hernandez, D. Streubel, K. Altendorf, and C. L. Lopez Gonzalez. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963−966.

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

Laundré, J. W., L. Hernández, and S. G. Clark. 2007. Numerical and demographic responses of lions to changes in prey abundance: testing current predictions. Journal of Wildlife Management 71:345−355.

Laundré, J. W., and L. Hernández. 2007. Do female pumas *(Puma concolor)* exhibit a birth pulse? Journal of Mammalogy 88:1300−1304.

Laundré, J. W. 2010. Behavioral response races, predator−prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. Ecology 9:2995−3007.

Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. United States Department of Agriculture Circular. 118:1−4.

Lindzey, F. G., W. D. Van Sickle, S. P. Laing, and C. S. Mecham. 1992. Cougar population response to manipulation in southern Utah. Wildlife Society Bulletin 20:224−227.

Lindzey, F. G., W. D. Van Sickle, B. B. Ackerman, D. Barnhurst, T. P. Hemker, and S. P. Laing. 1994. Cougar population dynamics in southern Utah. Journal of Wildlife Management 58:619−624.

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

Logan, K. A. 2019. Puma population limitation and regulation: What matters in puma management? Journal of Wildlife Management 83:1652−1666.

Lotz, M. 2017. Florida mountain lion status report. Pages 85−92 *in* C. R. McLaughlin and M. Vieira, editors. Proceedings of the 12th Mountain Lion Workshop. Estes Park, Colorado, USA.

Maehr, D. S. 1997. The Florida panther: Life and death of a vanishing carnivore. Island Press, Washington, D. C., USA.

Manfredo, M. J., L. Sullivan, A. W. Don Carlos, A. M. Dietsch, T. L. Teel, A. D. Bright, and J. Bruskotter. 2018. America's wildlife values: The social context of wildlife management in the U.S. National report for the Western Association of Fish and Wildlife Agencies and the Midwest Association of Wildlife Agencies. Department of Human Dimensions of Natural Resources, Colorado State University, Fort Collins, USA.

Martorello, D. A., and R. A. Beausoleil. 2003. Characteristics of cougar harvest with and without the use of dogs. Pages 129−135 *in* Proceedings of the Seventh Mountain Lion Workshop, Jackson, Wyoming, USA.

Mattson, D. J., and T. Merrill. 2002. Extirpations of grizzly bears in the contiguous United States, 1850−2000. Conservation Biology 16:1123−1136.

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

May, W. L., and W. D. Johnson. 1997. A SAS macro for constructing simultaneous confidence intervals for multinomial proportions. Computer Methods and Programs in Biomedicine 53:153−162.

McRae, B. H., P. Beier, L. E. DeWald, L. Y. Huynh, and P. Keim. 2005. Habitat barriers limit gene flow and illuminate historical events in a wide-ranging carnivore, the American puma. Molecular Ecology 14:1965−1977.

Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, The American Museum of Natural History, Garden City, New York, USA.

Milner, J. M., E. B. Nilsen, and H. P. Andreassen. 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21:36−47.

Montana Fish, Wildlife and Parks. 2018. Montana gray wolf conservation and management 2017 annual report. Montana Fish, Wildlife and Parks. Helena, USA.

Montana Fish, Wildlife and Parks. 2019. Montana mountain lion monitoring and management strategy. Montana Fish, Wildlife and Parks. Helena, USA.

Moss, W. E., M. W. Alldredge, and J. N. Pauli. 2016. Quantifying risk and resource use for a large carnivore in an expanding urban−wildland interface. Journal of Applied Ecology 53:371−378.

Murphy, K. M. 1998. The ecology of the cougar *(Puma concolor)* in the Northern Yellowstone Ecosystem: interactions with prey, bears, and humans. Dissertation, University of Idaho, Moscow, USA.

Musiani, M., and P. C. Paquet. 2004. The practices of wolf, persecution, protection, and restoration in Canada and the United States. Bioscience 54:50−60.

Mysterud, A. 2011. Selective harvesting of large mammals: how often does it result in directional selection? Journal of Applied Ecology 48: 827−834.

Nadeau, S. Idaho mountain lion status report. 2008. Pages 8−17 *in* Proceedings of the 9th Mountain Lion Workshop. D. Toweill, S. Nadeau, and D. Smith, editors. 5−8 May 2008, Sun Valley, Idaho, USA.

Negri, S., and H. Quigley. 2010. Cougar conservation: the growing role of citizens and government. Pages 221−234 *in* Cougar: ecology & conservation, M. Hornocker and S. Negri, editors. University of Chicago Press, Chicago, Illinois, USA.

Newbolt, C. H., P. K. Acker, T. J. Neuman, S. I. Hoffman, S. S. Ditchkoff, and T. D. Steury. 2017. Factors influencing reproductive success in male white-tailed deer. Journal of Wildlife Management 81:206−217.

Newby, J. R., L. S. Mills, T. K. Ruth, D. H. Pletscher, M. S. Mitchell, H. B. Quigley, K. M. Murphy, and R. DeSimone. 2013. Human-caused mortality influences spatial population dynamics: pumas in landscapes with varying mortality risks. Biological Conservation 159:230−239.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Carnivore biology and carnivore conservation in the Rocky Mountains. Conservation Biology 10:949−963.

Novaro, A. J., M. C. Funes, and R. S. Walker. 2005. An empirical test of source−sink dynamics induced by hunting. Journal of Applied Ecology 42:910−920.

Nowak, R. M. 1976. The cougar in the United States and Canada. U.S. Department of Interior Fish and Wildlife Service, Washington D. C., and New York Zoological Society, New York, USA.

Onorato, D., R. DeSimone, C. White, and L. P. Waits. 2011. Genetic assessment of paternity and relatedness in a managed population of cougars. Journal of Wildlife Management 75:378−384.

Organ, J. F., V. Geist, S. P. Mahoney, S. Williams, P. R. Krausman, G. R. Batcheller, T. A. Decker, R. Carmichael, P. Nanjappa, R. Regan, R. A. Medellin, R. Cantu, R. E. McCabe, S. Craven, G. M. Vecellio, and D. J. Decker. 2012. The North American Model of Wildlife Conservation. The Wildlife Society Technical Review 12-04. The Wildlife Society, Bethesda, Maryland, USA.

Pavlik, S. 2000. Will big trotter reclaim his place? The role of the wolf in Navajo tradition. American Indian Culture and Research Journal 24:107−125.

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. The Wildlife Society Technical Review 12−1. The Wildlife Society, Bethesda, Maryland, USA.

Pelton, M. R. 2000. Black bear. Pages 389−408 *in* Ecology and management of large mammals in North America, S. Demarais and P. R. Krausman, editors. Prentice Hall, Inc., Upper Saddle River, New Jersey, USA.

Petersen, C. G. J. 1896. The yearly immigration of young plaice into the Limfjord from the German Sea. Report of the Danish Biological Station 6:5−84.

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.

Pierce, B. M., V. C. Bleich, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. Journal of Mammalogy 93:977−988.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7−15.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107.

Proffitt, K. M., J. F. Goldberg, M. Hebblewhite, R. Russell, B. S. Jiminez, H. S. Robinson, K. Pilgrim, and M. K. Schwartz. 2015. Integrating resource selection into spatial capture-recapture models for large carnivores. Ecosphere 6:1−15.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652−661.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

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., and R. DeSimone. 2011. The Garnet Range mountain lion study: Characteristics of a hunted population in west-central Montana. Final report, Federal Aid in Wildlife Restoration Project W-154-R. Montana Fish, Wildlife and Parks, Helena, USA.

Robinson, H. S., R. Desimone, C. Hartway, J. A. Gude, M. J. Thompson, M. S. Mitchell, and M. Hebblewhite. 2014. A test of the compensatory mortality hypothesis in mountain lions: a management experiment in west-central Montana. Journal of Wildlife Management 78:791−807.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417−426.

Runge, J. P., M. C. Runge, and J. D. Nichols. 2006. The role of local populations within a landscape context: defining and classifying sources and sinks. American Naturalist 167:925−938.

Ruth, T. K., and K. Murphy. 2010. Cougar-prey relationships. Pages 138−162 in Cougar: ecology & conservation, M. Hornocker and S. Negri, editors. Chicago Press, Chicago, Illinois, USA.

Ruth, T. K., M. A. Haroldson, K. M. Murphy, P. C. Buotte, M. G. Hornocker, and H. B. Quigley. 2011. Cougar survival and source-sink structure on Greater Yellowstone's Northern Range. Journal of Wildlife Management 75:1381−1398.

Ruth, T. K., P, C. Buotte, and M. G. Hornocker. 2019. Yellowstone cougars: ecology before and during wolf restoration. University Press of Colorado, Louisville, USA.

Scheick, B. K., and W. McCowan. 2014. Geographic distribution of American black bears in North America. Ursus 25:24−33.

Schwartz, C. C., and K. Gunther. 2006. Grizzly bear management in Yellowstone National Park: the heart of the recovery in the Yellowstone Ecosystem. Pages 232−238 in Wildlife in Shiretoko and Yellowstone National Parks: lessons in wildlife conservation from two World Heritage Sites. D. R. McCullough, K. Kaji, and M. Yamanaka, editors. Shiretoko Nature Foundation, Hokkaido, Japan.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, Second edition. MacMillan, New York, USA.

Seidensticker, J. C., M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35.

Sikes, R. S., the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild animals in research and education. Journal of Mammalogy 97:663−688.

Sinnock, S. 1978. Geomorphology of the Uncompahgre Plateau and Grand Valley, western Colorado, U.S.A. Dissertation, Purdue University, West Lafayette, Indiana, USA.

Spreadbury, B. R., K. Musil, J. Musil, C. Kaisner, and J. Kovak. 1996. Cougar population characteristics in southeastern British Columbia. Journal of Wildlife Management 60:962−969.

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

Stoner, D. C., M. L. Wolfe, C. Mecham, M. Mecham, S. Durham, and D. M. Choate. 2013. Dispersal behavior of a polygynous carnivore: do cougars *Puma concolor* follow source-sink predictions? Wildlife Biology 19:289−301.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798−808.

Sweanor, L. L., K. A. Logan, J. W. Bauer, B. Millsap, and W. M. Boyce. 2008. Puma and human spatial and temporal use of a popular California State Park. Journal of Wildlife Management 72:1076−1084.

Teel, T. L., R. S. Krannich, and R. H. Schmidt. 2002. Utah stakeholder's attitudes toward selected cougar and black bear management practices. Wildlife Society Bulletin 30:2−15.

Teel, T. L., and M. J. Manfredo. 2009. Understanding the diversity of public interests in wildlife conservation. Conservation Biology 24:128−139.

Tenhumberg, B. A., A. J. Tyre, A. R. Pople, and H. Possingham. 2004. Do harvest refuges buffer kangaroos against evolutionary responses to selective harvesting? Ecology 85:2003−2017.

Thompson, D. J., J. A. Jenks, and D. M. Fecske. 2014. Prevalence of human-caused mortality in an unhunted cougar population and potential impacts to management. Wildlife Society Bulletin 38:341−347.

Updike, D. 2005. California mountain lion status report. Pages 41−48 *in* R. A. Beausoleil and

D. A. Martorello, editors. Proceedings of the Eighth Mountain Lion Workshop, Olympia, Washington, USA.

U.S. Fish and Wildlife Service. 2018. Endangered and threatened wildlife and plants; removing the Eastern Puma (=Cougar) from the Federal List of Endangered and Threatened Wildlife. Federal Register 83:3086.

Van de Kerk, M., D. P. Onorato, J. A. Hostetler, B. M. Bolker, and M. K. Oli. 2019. Dynamics, persistence, and genetic management of the endangered Florida panther population. Wildlife Monographs 203:3−35.

Vickers, T. W., J. N. Sanchez, C. K. Johnson, S. A. Morrison, R. Botta, T. Smith, B. S. Cohen, P. R. Huber, H. B. Ernest, and W. M. Boyce. 2015. Survival and mortality of pumas *(Puma concolor)* in a fragmented, urbanizing landscape. PloS One 10(7): e0131490. doi:10.1371/journal.pone.0131490.

Walters, C. 1986. Adaptive management of renewable resources. Macmillan Publishing, New York, New York, USA.

Wharton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794−800.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Suppl):S120−S139.

White, G. C., and B. C. Lubow. 2002. Fitting population models to multiple sources of observed data. Journal of Wildlife Management 66:300−309.

Whittaker, D. G. 2005. Oregon mountain lion status report. Pages 11−16 *in* R. A. Beausoleil and D. A. Martorello, editors. Proceedings of the Eighth Mountain Lion Workshop, Olympia, Washington, USA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. Analysis and management of animal populations. Academic Press, New York, New York, USA.

Wolfe, M. L., D. N. Koons, D. C. Stoner, P. Terletzky, E. M. Gese, D. M. Choate, and L. M. Aubrey. 2015. Is anthropogenic cougar mortality compensated by changes in natural mortality in Utah? Insight from long-term studies. Biological Conservation 182:187−196.

Wolfe, M. L., E. M. Gese, P. Terletzky, D. Stoner, and L. M. Aubry. 2016. Evaluation of harvest indices for monitoring cougar survival and abundance. Journal of Wildlife Management 80:27−36.

Woodruffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126−2128.

Wyoming Game and Fish. 2006. Mountain lion management plan. Wyoming Game and Fish Department, Lander, USA.

Young, S. P., and E. A. Goldman. 1944. The wolves of North America, Part I: their history, life habits, economic status, and control. Dover Publications, Inc., New York, New York, USA.

Young, S. P., and E. A. Goldman. 1946. The puma: mysterious American cat. The American Wildlife Institute, Washington, D. C., USA.

Appendix I. Puma population models used to project an estimated number of independent pumas in treatment year 1 (TY1, 2009−2010) and treatment year 4 (TY4, 2012−13) to set experimental harvest quotas, Uncompahgre Plateau Study Area (UPSA), Colorado, USA.

Model for TY1 projection
Research on pumas on the UPSA from December 2004 to July 2007 provided estimates of puma population structure and parameters for a model-based approach to project expected abundance of independent pumas to set the initial 15% harvest for TY1. The life stage-structured, deterministic, discrete time model was:

N_{t+1} = Adult Females + Adult Males + Subadult Females + Subadult Males + Cubs

$N_{t+1} = [(S_{AF} \times N_{AFt}) + (S_{SF} \times N_{SFt})] + [(S_{AM} \times N_{AMt}) + (S_{SM} \times N_{SMt})] + [(r \times S_C \times N_{Ct}) \times PI_{SF} / E_{SF}] + \{[(1 - r) \times S_C \times N_{Ct}] \times PI_{SM} / E_{SM} \} + (L_{\bar{y}} \times AF_R \times N_{AFt+1})$

Terms:
N_{AFt} = Number of adult females at year t.
N_{AMt} = Number of adult males at year t.
N_{SFt} = Number of subadult females at year t.
N_{SMt} = Number of subadult males at year t.
N_{Ct} = Number of cubs at year t.
S = Survival rate for each specified sex and life stage.
r = Proportion of the subadult population that is female.
PI/E = Ratio of progeny + immigrants / emigrants.
$L_{\bar{y}}$ = Average litter size.
AF_R = Proportion of adult females giving birth to new litters each year.
Assumptions of the model included: 1) expected puma population projections were conditional on the assigned puma population structure and demographic estimates from our data from reference year 1 (RY1) to reference year 4 (RY4), 2004−2008. The starting population was the count of independent pumas (i.e., adults and subadults) and estimated sex and age structure made during November 2007 to March 2008 (RY4, 33 pumas). 2) Density dependence did not operate in this model. This model projected an expected 53 independent pumas in TY1. We set the quota for TY1 at 8 independent pumas to represent the 15% target harvest on the independent pumas (i.e., $53 \times 0.15 = 7.95$).

Model for TY4 projection
When a linear decline in the abundance of independent pumas was detected during treatment year 1 (TY1) to treatment year 3 (TY3) we used linear regression on the independent puma counts for TY1−TY3 to project an expected abundance in treatment year 4 (TY4). The linear regression model was:
$y = -4x + 60$, $R^2 = 1.0$. The projected abundance of independent pumas in TY4 was 44.

Appendix II.
Minimum counts of independent pumas (i.e., adults and subadults) each November through March, reference period year 4 (RY4) to treatment period year 3 (TY3), 2007−2012, on the Uncompahgre Plateau Study Area, Colorado, USA. Minimum counts of pumas were based on numbers of known radio-collared pumas, visual observations of captured non-marked pumas, harvested non-marked pumas, and from track counts of suspected unique non-marked pumas on the study area.

Study year	Time span	Adults		Subadults		Total independent pumas
		Female	Male	Female	Male	
RY4	Nov 2007−Mar 2008	16	8	5	4	33
RY5	Nov 2008−Mar 2009	20−23	9−10	3−6	1−2	37
TY1	Nov 2009−Mar 2010	30	20	1	4	55
TY2	Nov 2010−Mar 2011	30	12	5	5	52
TY3	Nov 2011−Mar 2012	27	9	4	8	48

Appendix III. Survival models developed in program MARK for the adult, subadult, and cub life stages of pumas on the Uncompahgre Plateau Study Area, Colorado, USA, 2005−2014.

Table AIII. 1. Adult puma survival modeling results, 2005−2014, Uncompahgre Plateau, Colorado, USA.

Model	AIC_c	ΔAIC_c	AIC_c weight[a]	Model Likelihood	No. Parameters	Deviance
Sex × Period	396.987	0	0.492	1	4	162.038
M × Period (Fconstant)	397.427	0.440	0.395	0.803	3	164.486
Sex + Period	401.613	4.626	0.049	0.099	3	168.672
Sex × Year	402.161	5.173	0.0372	0.075	14	147.002
M × Year (Fconstant)	403.481	6.494	0.019	0.039	10	156.433
Period	405.339	8.352	0.008	0.015	2	174.404
Sex + Year	409.319	12.332	0.001	0.002	10	162.271
Sex	416.748	19.760	0.000	0.000	2	185.813
Constant	417.378	20.390	0.000	0	1	188.448

Table AIII. 2. Subadult puma survival modeling results, 2005−2014, Uncompahgre Plateau, Colorado, USA.

Model	AIC_c	ΔAIC_c	AIC_c weight[a]	Model Likelihood	No. Parameters	Deviance
M × Period (Fconstant)	188.133	0	0.561	1	3	39.580
Sex × Period	190.068	1.935	0.213	0.380	4	39.487
Period	191.125	2.992	0.126	0.224	2	44.593
Sex + Period	192.130	3.997	0.076	0.136	3	43.577
Constant	195.224	7.091	0.016	0.029	1	50.707
Sex	196.676	8.543	0.007	0.014	2	50.144
Month × Period	206.577	18.444	0.000	0.000	24	13.888
Month × Sex	209.631	21.498	0.000	0.000	24	16.942
Month × Period × Sex	266.488	78.355	0.000	0.000	48	0.000

Table AIII. 3. Puma cub survival modeling results, 2005−2014, Uncompahgre Plateau, Colorado, USA.

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Model Likelihood	No. Parameters	Q Deviance
MotherId	201.473	0	0.366	1	2	197.453
Sex + MotherId	203.331	1.859	0.144	0.395	3	197.292
Period + MotherId	203.426	1.953	0.136	0.377	3	197.386
Period × Sex + MotherId	203.457	1.985	0.136	0.371	5	193.358
Sex × MotherId	204.634	3.161	0.075	0.206	4	196.567
Period × MotherId	205.077	3.605	0.060	0.165	4	197.011
Constant	206.617	5.144	0.028	0.076	1	204.610
Period	207.287	5.814	0.020	0.055	2	203.267
Period × Sex	208.174	6.701	0.013	0.035	4	200.108
Sex	208.315	6.843	0.012	0.033	2	204.296
Sex + Period	208.923	7.451	0.009	0.024	3	202.884

Appendix IV. Estimated annual and life stage puma survival rates in hunted and non-hunted populations in North America, 1992−2020.

Location	Adults No hunting	Adults Hunting	Subadults No hunting	Subadults Hunting	Cubs	Reference
Colorado	0.86 F	0.74 F	0.63 F	0.70 F	0.51[a]	This study
	0.96 M	0.40 M	0.92 M	0.43 M	0.14[b]	
Colorado	NA[c]	0.69−0.92 F and M	NA	0.64 F and M	NA	Anderson et al. 1992
Colorado	NA	0.77 F	NA	NA	NA	Moss et al. 2016
		0.63 M				
California	0.56[d]	NA	0.56[d]	NA	0.56[d]	Vickers et al. 2015
Florida	0.87 prime F	NA	0.95 F	NA	0.32	Hostetler et al. 2010
	0.76 old F		0.71 M			Benson et al. 2011
	0.80 prime M					
	0.64 old M					
New Mexico	0.82 F	NA	0.88 F	NA	0.64	Logan and Sweanor 2001
	0.91 M		0.56 M			
Utah	NA	0.64 F and M[e]	NA	NA	NA	Stoner et al. 2006
		0.76 F and M[f]				
British Columbia, Idaho and Washington	NA	0.77 F	NA	0.32 F	NA	Lambert et al. 2006
		0.59 M		0.37 M		
Idaho and Utah	NA	0.93 F[g]	NA	NA	0.86[g]	Laundre et al. 2007
		0.78 F[h]			0.57[h]	
Washington		0.87 F[i]	NA	0.76 F[i]	0.72 F[i]	Cooley et al. 2009*a*
		0.65 M[i]		0.51 M[i]	0.53 M[i]	
		0.66 F[j]		1.00 F[j]	0.32 F[j]	
		0.48 M[j]		0.54 M[j]	0.31 M[j]	
Greater Yellowstone Northern Range	NA	0.88 F[k]	NA	NA	0.46[k]	Ruth et al. 2011
		0.75 M[k]			0.59[l]	
		0.84 F[l]				
		0.68 M[l]				
Montana	NA	0.67 F	NA	0.49 F	0.49 F	Robinson and DeSimone 2011
		0.72 M		0.39 M	0.76 M	
South Dakota	0.90 F	0.79 F			0.52[m]	Jansen 2011
	0.70 M	0.40 M				
	0.86 F	NA	1.0 F	NA	0.67	Thompson et al. 2014
	0.89 M		0.63 M			

Oregon	NA	0.84−0.86 F[n] 0.57 M[o] 0.78−0.86 M[p]	NA		0.66	Clark et al. 2014, 2015
Wyoming	0.89[q]	0.82[r]	0.87[q]	0.85[r]	0.44[q] 0.28[r]	Elbroch et al. 2018

[a]Mothers lived.
[b]Mothers died.
[c]NA: Not Applicable.
[d]Survival was constant across age stage, gender, and population segment.
[e]Monroe Mts., Utah.
[f]Oquirrh Mts., Utah.
[g]Before deer decline.
[h]After deer decline.
[i]Light puma hunting.
[j]Heavy puma hunting.
[k]Prior to wolf presence. Adult and subadult pumas were combined.
[l]During wolf presence. Adult and subadult pumas were combined.
[m]Pumas were hunted.
[n]Puma hunting with and without dogs. Adult and subadult pumas were combined.
[o]Puma hunting with dogs. Adult and subadult pumas were combined.
[p]Puma hunting without dogs. Adult and subadult pumas were combined.
[q]Sexes were pooled across years; survival estimate for the non-hunting season (1 Apr−30 Sep).
[r]Sexes were pooled across years; survival estimate for the hunting season (1 Oct−31 Mar).

Appendix V. Puma reproduction parameter estimates in hunted and non-hunted populations in North America, 1983−2020.

Parameter	Average	Hunting status	Range	95% CI	Sample sizes	State or Province	Reference
Gestation (days)	90.4_{min}−91.8_{max}	Combined[a]	84−95	89.1_{min}−92.9_{max}	17 litters, 13 mothers	CO	This study
	91.9	NA[b]	84−98	90.6−93.2	42 litters	Various	Anderson 1983
	91.5	Combined	83−103	90.1−92.9	31 litters, 18 mothers	NM	Logan and Sweanor 2001
Birth interval (mo.)	18.3	No hunting	11.7−23.9	15.5−21.1	17 intervals, 10 mothers	CO	This study
	19.4	Hunting	11.0−34.7	16.2−22.6	13 intervals, 10 mothers		
	17.4	Combined	12.6−22.1	16.2−18.6	16	NM	Logan and Sweanor 2001
	17.4	Hunting	11.5−24.0	NA	12	NV	Ashman et al. 1983
	24.3	No hunting	19−40	19.3−29.3	7	UT	Lindzey et al. 1994
	19.7	Hunting	12−32	NA	12	AB	Ross and Jalkotzy 1992
	19.8	Combined	NA	16.5−23.0	NA	MT	Robinson et al. 2014
Age at 1st conception (mo.)	28.7	Combined	18−45	24.1−33.2	14	CO	This study
	27.0	Hunting	21−34	NA	6	AB	Ross and Jalkotzy 1992
	26.1	Combined	19−37	22.7−29.5	12	NM	Logan and Sweanor 2001
	23.0	No hunting	17 min.[c]	19.4−26.6	6	UT	Lindzey et al. 1994
	28.4	Combined	20−34	NA	14	MT	Robinson et al. 2014
Age at 1st litter (mo.)	31.7	Combined	21−48	27.1−36.3	14	CO	This study
	29.1	Combined	22−40	25.7−32.5	12	NM	Logan and Sweanor 2001
	26.0	No hunting	20 min.[c]	22.4−29.6	6	UT	Lindzey et al. 1994
	31.4	Combined	23−37	NA	14	MT	Robinson et al. 2014
Litter size (nurslings)	2.8	No hunting	1−4	2.41−3.12	26 litters/14 mothers	CO	This study
	2.4	Hunting	1−4	1.99−2.76	21 litters/16 mothers		
	3.1	Hunting	1−5	NA	36 prenatal litters	NV	Ashman et al. 1983
	2.4	No hunting	1−4	1.6−3.2	26 litters	UT	Lindzey et al. 1994

Metric							
	3.0	Combined	2−4	2.8−3.2	53 litters	NM	Logan and Sweanor 2001
	2.5	Hunting	NA	1.99−3.0	15 litters	WA	Lambert et al. 2006
	2.5	Hunting	NA	2.1−2.9	15 litters	WA	Cooley et al. 2009a
	3.0	No hunting	2−4	2.5−3.5	8 litters	SD	Jansen 2011
	2.9	Hunting	2−4	2.6−3.2	26 litters		
	2.9	Combined	NA	2.7−3.1	24 litters	MT	Robinson et al. 2014
M:F cub sex ratio	41:31	No hunting	NA	NA	72 nurslings	CO	This study
	27:22	Hunting	NA	NA	49 nurslings		
	75:73	Combined	NA	NA	148 nurslings	NM	Logan and Sweanor 2001
	1:1.13	Hunting	NA	NA	17 cubs	WA	Lambert et al. 2006
	33:37	Hunting	NA	NA	70 nurslings	SD	Jansen 2011
Parturition rate	0.63	No hunting	NA	0.49−0.75	12−13 mothers, 4 yrs	CO	This study
	0.48	Hunting	NA	0.37−0.59	13−17 mothers, 5 yrs		
	0.48	No hunting	0.21−0.73	NA	7 yrs	NM	Logan and Sweanor 2001
	0.52	Removal[d]	0.29−0.75	NA	7 yrs		
	0.44	Heavy hunting	NA	NA	6 yrs	WA	Cooley et al. 2009a
	0.51	Light hunting	NA	NA	6 yrs		
	0.58	Combined	NA	NA	9 yrs	MT	Robinson and DeSimone 2011

[a]Combined: data were compiled over hunted and non-hunted time periods.
[b]NA: Not Applicable.
[c]A minimum quantity was reported.
[d]Pumas were removed alive and translocated, resulting in a one-half reduction in the adult puma population.