Effects of Hunting on a Puma Population in Colorado

KENNETH A. LOGAN,[1] *Colorado Parks and Wildlife, 2300 S. Townsend Avenue, Montrose, CO 81401, USA*

JONATHAN P. RUNGE, *Colorado Parks and Wildlife, 317 W. Prospect Road, Fort Collins, CO 80526, USA*

ABSTRACT We investigated effects of regulated hunting on a puma (*Puma concolor*) population on the Uncompahgre Plateau (UPSA) in southwestern Colorado, USA. We examined the hypothesis that an annual harvest rate averaging 15% of the estimated number of independent individuals 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 animals. 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 hunting. We captured and marked pumas on the UPSA and monitored them year-round to examine their demographics, reproduction, and movements. We estimated abundance of independent animals using the UPSA each winter during the Colorado hunting season from reference year 2 (RY2) to treatment year 5 (TY5) using the Lincoln-Petersen method. In addition, we surveyed hunters to investigate how their behavior influenced harvest and the population. We captured and marked 110 and 116 unique pumas in the reference and treatment periods, respectively, during 440 total capture events. Those animals produced known-fate data for 75 adults, 75 subadults, and 118 cubs, which we used to estimate sex- and life stage-specific survival rates. In the reference period, independent pumas more than doubled in abundance and exhibited high survival. Natural mortality was the major cause of death to independent individuals, 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 others on the UPSA. Abundance of independent pumas using the UPSA declined 35% after 4 years of hunting with harvest rates averaging 15% annually. Harvest rates at the population scale, including marked independent pumas with home ranges exclusively on the UPSA, overlapping the UPSA, and on adjacent management units were higher, averaging 22% annually in the same 4 years leading to the population decline. Adult females comprised 21% of the total harvest. The top-ranked model explaining variation in adult survival ($\hat{S}$) indicated a period effect interacting with sex. Annual adult male survival was higher in the reference period ($\hat{S} = 0.96$, 95% 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 model showed that female subadult survival was constant across the reference and treatment periods ($\hat{S} = 0.68$, 95% CI = 0.43–0.84), whereas survival of subadult males exhibited the same trend as that of adult males: 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 ($\hat{S}_{\text{mother alive}} = 0.51$, 95% CI = 0.35–0.66; $\hat{S}_{\text{mother died}} = 0.14$, 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; their abundance declined by 59% after 3 hunting seasons and we did not detect any males >6 years old after 2 hunting seasons. Pumas born on the UPSA that survived to subadult stage exhibited both philopatry and dispersal. Local recruitment and immigration contributed to positive 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 months, 95% CI = 15.5–21.1; treatment period = 19.4 months, 95% CI = 16.2–22.6), but 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. Successful hunters used dogs, selected primarily males, and harvested pumas in 1–2 days (median). We found that an annual 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 abundance. At this scale, annual mortality rates of independent animals 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 were largely additive and reproduction and recruitment did not compensate for this mortality source. Hunters generally selected male pumas, resulting in a decline in their survival and abundance, and the age structure of the population. We recommend that regulated hunting in a

[1]*E-mail: ken.logan@state.co.us*

source-sink structure be used to conserve puma populations, provide sustainable hunting opportunities, and address puma-human conflicts. © 2021 The Wildlife Society.

Efectos de la Cacería en una Población de Pumas en Colorado

RESUMEN Investigamos los efectos de la cacería regulada en la población de pumas (*Puma concolor*) de la Uncompahgre Plateau (UPSA) en el suroeste de Colorado, USA. Exploramos la hipótesis de que una cosecha anual con una tasa promedio del 15% del número estimado de pumas independientes que están usando el área de estudio resultaría en una abundancia estable o un incremento de pumas independientes. Nuestra predicción de que la mortalidad por cacería seria compensada por: 1) una reducción en otras causas de mortalidad, por lo tanto, la supervivencia se mantendría igual o incrementaría; 2) un incremento en la tasa reproductiva; o 3) un incremento en el reclutamiento de pumas jóvenes. Este estudio se llevó a cabo a lo largo de 10 años (2004–2014) y fue diseñado con un periodo de referencia (años 1 al 5; RY1–RY5) sin cacería de pumas y un periodo de tratamiento (años 6–10; i.e., TY1–TY5) con cacería de pumas. Capturamos y marcamos pumas en la UPSA y se llevó a cabo el monitoreo a lo largo de todo el año para examinar la demografía, reproducción y movimientos de los pumas. Estimamos la abundancia de pumas independientes que usaban la UPSA cada invierno durante la estación de cacería de pumas en Colorado usando el año 2 (RY2) como referencia al año de tratamiento 5 (TY5) usando el método de Lincoln-Petersen. Adicionalmente, llevamos a cabo prospecciones con cazadores para investigar como el comportamiento de los cazadores influía la cosecha y la población de pumas. Capturamos y marcamos un total de 110 y 116 pumas únicos dentro del periodos de referencia y de tratamiento, respectivamente, a lo largo de un total de 440 eventos de captura. Esos pumas produjeron datos de mortalidad con información conocida para 75 adultos, 75 sub-adultos y 118 cachorros, con los cuales se estimaron tasas de supervivencia específicas por sexo y etapas de vida. En el periodo de referencia la abundancia de pumas independientes se incrementó a más del doble y exhibieron una supervivencia alta. La mortalidad natural fue la mayor causa de muerte en pumas independientes, seguida de causas producidas por seres humanos (e.g. atropellamientos, control de depredadores). En el periodo de tratamiento, los cazadores mataron 35 pumas independientes, adicionalmente capturaron y dejaron en libertad a 30 pumas en la UPSA. La abundancia de pumas independientes se redujo en un 35% después de 4 años de cacería con tasas de aprovechamiento con un promedio anual de 15% en la UPSA. Las tasas de aprovechamiento a la escala de población incluyendo pumas independientes marcados con ámbitos hogareños exclusivos dentro de la UPSA, con sobreposición en la UPSA y en unidades adyacentes de manejo fueron mayores, en promedio 22% anualmente durante los mismos 4 años que llevaron a la población al declive. Las hembras adultas comprendieron 21% de la cosecha total. El mejor modelo que explicaba la variación en la supervivencia ($\hat{S}$) de los adultos indicaba un efecto del periodo interactuando con el sexo. La supervivencia anual de los machos fue más alta durante el periodo de referencia ($\hat{S} = 0.96$, 95% CI = 0.75–0.99) que durante el periodo de tratamiento ($\hat{S} = 0.40$, 95% CI = 0.22–0.57). La supervivencia anual de las hembras fue 0.86 (95% CI = 0.72–0.94) en el periodo de referencia y 0.74 (95% CI = 0.63–0.82) durante el tratamiento. El mejor modelo de supervivencia en hembras sub-adultas, mostro que la supervivencia fue constante a través de los periodos de referencia y tratamiento ($\hat{S} = 0.68$, 95% CI = 0.43–0.84), donde la supervivencia de los machos sub-adultos exhibió el mismo patrón de supervivencia de los machos adultos: más alta en el periodo de referencia ($\hat{S} = 0.92$, 95% CI = 0.57–0.99) y menor en el periodo de tratamiento ($\hat{S} = 0.43$, 95% CI = 0.25–0.60). La supervivencia de los cachorros se explica mejor por el destino de sus madres, cuando estos son dependientes ($\hat{S}_{\text{madres vivas}} = 0.51$, 95% CI = 0.35–0.66; $\hat{S}_{\text{madres muertas}} = 0.14$, 95% CI = 0.03–0.34). La distribución por edades de los pumas independientes estuvo sesgada a animales jóvenes durante el periodo de tratamiento. Los machos adultos fueron los más afectados por el aprovechamiento, su abundancia se redujo en un 59% después de 3 temporadas de cacería, y una ausencia de machos >6 años de edad después de 2 temporadas de cacería. Los pumas nacidos en la UPSA que sobrevivieron a la etapa sub-adulta exhibieron características filopátricas y de dispersión. El reclutamiento local y la inmigración contribuyeron al crecimiento positivo en el periodo de referencia. Sin embargo, el reclutamiento no compenso por la pérdida de machos adultos y parcialmente compenso por la pérdida de hembras durante el periodo de tratamiento. El intervalo promedio entre nacimientos fue similar entre los periodos de referencia y tratamiento (periodo de referencia = 18.3 meses, 95% CI = 15.5–21.1; periodo de tratamiento = 19.4 meses, 95% CI = 16.2–22.6), mientras que el tamaño de camada (periodos de referencia = 2.8, 95% CI = 2.4–3.1; periodo de tratamiento = 2.4, 95% CI = 2.0–2.8) y las tasas de parición (periodo de referencia = 0.63, 95% CI = 0.49–0.75; periodo de tratamiento = 0.48, 95% CI = 0.37–0.59) declinaron ligeramente durante el periodo de tratamiento. Cazadores exitosos de pumas usaron perros, seleccionaron fundamentalmente machos y cosecharon pumas en 1–2 días (mediana). Encontramos a la escala de población una tasa de aprovechamiento anual de 22% del número de pumas independientes en un periodo de 4 años y donde >20% de

hembras adultas en la cosecha total redujeron en cantidad la abundancia de pumas. A esta escala, las tasas anuales de mortalidad de los pumas independientes por cacería fueron en promedio 6.3 veces mayores que todas las otras causas producidas por seres humanos, y 4.6 veces mayores que todas las causas de mortalidad natural durante la reducción en la población. La mortalidad por cacería era aditiva y la reproducción y el reclutamiento no compensaron a la mortalidad por cacería. Encontramos que los cazadores de pumas seleccionaron pumas machos, resultando en una reducción de la supervivencia, abundancia de machos y la estructura de edades dentro de la población. Recomendamos que la cacería regulada con base en una estructura poblacional de fuente-sumidero puede ser utilizada para conservar a las poblaciones de pumas, proporcionando oportunidades para la cacería sustentable de pumas y redirigir el conflicto entre pumas y seres humanos.

Effets de la Chasse sur une Population de Puma au Colorado

RÉSUMÉ Nous avons examiné les effets d'une chasse régulée sur une population de puma (*Puma concolor*) dans le plateau de l'Uncompahgre (UPSA) dans le sud-ouest du Colorado. Nous avons examiné l'hypothèse qu'un taux annuel de récolte de 15% du nombre estimé de pumas indépendants utilisant l'aire d'étude maintiendrait l'abondance ou accroîtrait l'abondance de pumas. Nous avons prédit que la mortalité par la chasse serait compensée par: 1) une réduction des autres causes de mortalité, entrainant une augmentation ou stabilisation de la survie; 2) une augmentation du taux de reproduction; ou 3) une augmentation du recrutement de jeunes individus. L'étude a été conduit durant, et a été construite autour d'une période de référence (années 1 à 5) sans chasse aux pumas et une période de traitement (années 6 à 10) avec une chasse aux pumas. Nous avons capturé et marqué des pumas dans l'aire d'étude (UPSA) et les avons suivis toute l'année pour récolter des données concernant leur démographie, reproduction et mouvement. L'abondance de pumas indépendants a été estimée dans l'USPA à chaque hiver durant la saison de chasse aux pumas au Colorado de l'année de référence 2 (RY2) à l'année de traitement 5 (TY5) en utilisant la méthode de Lincoln-Petersen. De plus, nous avons sondé les chasseurs afin d'apprendre comment leur comportement influençait la récolte et la population de puma. Durant les périodes de référence et traitement, 110 et 116 pumas ont respectivement été capturés et marqués, durant 440 évènements de capture. Ces pumas ont produit des données dont le sort est connu pour 75 adultes, 75 subadultes, et 118 juvéniles qui ont été utilisés afin de modéliser le taux de survie de chaque sexe et groupe d'âge. Durant la période de référence, l'abondance des pumas indépendants a plus que doublé en abondance et montré un haut taux de survie. La mortalité naturelle était la cause principale de décès, suivie par les mortalités reliées à l'humain. Durant la période de traitement, les chasseurs ont tué 35 pumas indépendants et capturé puis relâché 30 pumas. L'abondance de pumas indépendants a décliné de 35% après 4 années de chasse avec des taux de récolte moyennant 15% dans l'UPSA. Les taux de récoltes à l'échelle de la population incluant des individus dont le domaine vital était à l'intérieur de l'USPA, chevauchant l'USPA, ou en périphérie de l'USPA étaient plus élevés et approchaient 22% durant les quatre années précédant le déclin de la population. Les femelles adultes représentaient 21% de la récolte total. Le meilleur modèle expliquant la variation dans la survie ($\hat{S}$) des adultes incluait un effet de la période en interaction avec le sexe. Le taux de survie des mâles adultes était plus élevé durant la période de référence ($\hat{S} = 0.96$, 95% CI = 0.75–0.99) que durant la période de traitement ($\hat{S} = 0.40$, 95% CI = 0.22–0.57). Le taux de survie des femelles adultes était de 0.86 (95% CI = 0.72–0.94) durant la période de référence et de 0.74 (95% CI = 0.63–0.82) durant la période de traitement. Le meilleur modèle du taux de survie des femelles subadultes a démontré que la survie était constante entre les deux périodes de traitement ($\hat{S} = 0.68$, 95% CI = 0.43–0.84) alors que le taux de survie des mâles subadultes a montré la même tendance que les mâles adultes: plus élevé durant la période de référence ($\hat{S} = 0.92$, 95% CI = 0.57–0.99) que durant la période de traitement ($\hat{S} = 0.43$, 95% CI = 0.25–0.60). Le taux de survie des petits était le mieux expliqué par le sort de la mère alors que les petits étaient dépendants ($\hat{S}_{\text{mère en vie}} = 0.51$, 95% CI = 0.35–0.66; $\hat{S}_{\text{mère en vie}} = 0.14$, 95% CI = 0.03–0.34). La structure des âges des pumas indépendants a décliné durant la période de traitement. Les mâles adultes étaient les plus affectés par la récolte, leur abondance a décliné de 59% après trois saisons de chasse et aucun individu de plus de 6 ans n'était présent après deux saisons de chasse. Les pumas nés dans l'UPSA qui ont survécu au stage subadulte ont exhibé de la philopatrie et de la dispersion. Le recrutement local et l'immigration ont contribué au taux de croissance durant la période de référence. Le recrutement n'a pas compensé pour la perte de mâles adultes et a compensé partiellement pour la perte de femelles adultes durant la période de traitement. L'intervalle moyen des naissances est demeuré similaire (période de référence = 18.3 mo., 95% CI = 15.5–21.1; période de traitement = 19.4 mo., 95% CI = 16.2–22.6), alors que la taille des portées (période de référence = 2.8, 95% CI = 2.4–3.1; période de traitement = 2.4, 95% CI = 2.0–2.8) et le taux de parturition (période de

référence = 0.63, 95% CI = 0.49–0.75; période de traitement = 0.48, 95% CI = 0.37–0.59) ont diminué légèrement durant la période de traitement. Les chasseurs de pumas qui ont eu du succès ont utilisé des chiens, ils sélectionnaient primairement les mâles et ont récolté des pumas à l'intérieur de 1–2 jours (médiane). Nous avons trouvé qu'un taux de récolte moyen avoisinant 22% du nombre estimé de pumas indépendants sur quatre ans et avec >20% de femelles adultes dans la récolte réduisait grandement l'abondance de puma. À cette échelle, le taux de mortalité annuel provenant de la chasse était en moyenne 6.3 fois plus grand que le taux provenant de tous les autres causes de mortalité humaine et 4.6 fois plus grand que le taux de mortalité de source naturelle durant la période de déclin de la population. La mortalité par la chasse était largement additive et la reproduction et le recrutement n'ont pas compensé pour cette source de mortalité. Nous avons trouvé que les chasseurs montraient une sélection pour les pumas mâles, entrainant alors une réduction de la survie et de l'abondance des mâles et impactant la structure des âges de la population. Nous recommandons qu'une chasse régulée dans une structure source-puit peut être utilisée afin d'aider la conservation des pumas, procurer des opportunités de chasse durable, et adresser les conflits pumas-humains.

Contents

INTRODUCTION

Large carnivores in North America are managed and conserved based on public interests and institutional policies and actions (Young and Goldman 1946, Kellert et al. 1996, Pavlik 2000, Gill 2010, Clark et al. 2014*b*). 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 killed by humans for a variety of reasons: to mitigate potentially dangerous encounters with people, to reduce predation on 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*b*). 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, Teel and Manfredo 2009, Gill 2010, 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 other public benefits including human safety, protection of private property, and recreational hunting of the carnivores and their prey.

Large carnivores in the United States that are protected under the Endangered Species Act (ESA) have included the wolf,

grizzly bear, jaguar, 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. 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, and 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 public interest, including 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 (Updike 2005). In jurisdictions allowing hunting, state and provincial governments defined puma hunting seasons, and methods and amount of harvest. Restrictions on hunting apparently enabled populations to rebound from low numbers in the 1960s when, for example, 7 western states (CA, CO, ID, NM, OR, UT, and WA) each reported puma abundances in the hundreds (Cahalane 1964). By the early 2000s, those same states each reported puma abundances ranging from 2,000–6,000 (Becker et al. 2003, Whittaker 2005). As puma populations 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).

The ecological role of pumas is integral to wildlife management and conservation. Pumas affect the abundances, distributions, and behaviors 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 attitudes concerning recreational hunting of pumas vary (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 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 management objectives to ensure that puma populations hunted for recreation are sustainable, and to reduce their abundance where needed to mitigate 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.

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 without declining if that 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 hunting mortality is compensatory, the population is expected to increase or remain stable. If these mechanisms do not adequately compensate for hunting mortality, however, then puma harvest produces additive mortality to the extent that the population stops growing or declines over time. When this happens, hunting mortality limits population growth.

Information regarding the effects of hunting on puma populations is sparse. Researchers in Nevada claimed a sustainable puma harvest up to 30% but 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 there were 3 interceding years with no harvest so the annual sustainable harvest rate was unknown (Ross and Jalkotzy 1992).

The first experimental removal of pumas occurred in Utah in 1987–1989 with a 1-time removal of 6 individuals (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 further 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 populations (Logan and Sweanor 2001). The adult portions of 2 protected puma populations increased by average annual rates as high as 17–28% over 3 4-year periods after initial declines caused by culling. Logan and Sweanor (2001) found that population growth was apparently density dependent because average annual growth rates began to decline from 17% to 5% over 2 consecutive 4-year periods. The average annual observed rate of increase was 11%. The authors suggested that sustainable hunting mortality of the population should not exceed 11% of the adult pumas per year. Conversely, if the objective was population reduction, hunting mortality should exceed 11% of adults per year.

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 (CPW 2004). Managers assumed that to manage for a stable or increasing population, mortality rates of independent pumas (i.e., adults [usually >2 yr old] and subadults [immature animals independent from mothers, usually 1–2 yr old]) should be limited within the range of 8–15% of the expected abundance of independent animals. To reduce the population, managers assumed that mortality rates should be ≥16% (Apker 2005). Prior to our research, none of these hunting management assumptions had been tested for biological validity. To address this need, we examined effects of hunting on a population in Colorado. Because of logistical and funding constraints, we were unable to replicate this large-scale study on more than 1 geographic area. 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 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 population.

To best assist CPW managers, we posited that the upper mortality limit expected to result in a stable or increasing population was the most important variable to establish. 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; 2) no enhanced reproduction; and 3) no enhanced recruitment to fully compensate for hunting mortality. In addition, we investigated whether the behavior of hunters influenced harvest structure, and thus any emerging changes to puma population sex and age structure, by surveying hunters to gather information on their hunting methods and preferences.

STUDY AREA

The study area was the southern half of the Uncompahgre Plateau (in Mesa, Montrose, Ouray, and San Miguel counties of Colorado; Fig. 1), a montane highland oriented southeast to northwest and 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, $\bar{x}$ = 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 wildland.

Vegetation on the UPSA transitioned from foothills covered in pinion-juniper (pinyon pine [*Pinus edulis*] and juniper [*Juniperus* spp.]) woodlands starting at about 1,700 m in elevation to
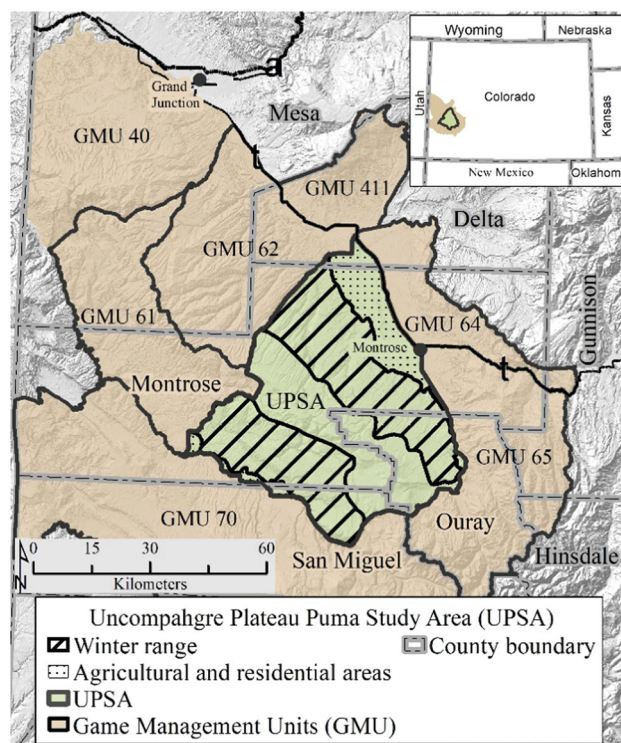
Figure 1. The Uncompahgre Plateau Study Area (UPSA) and surrounding Game Management Units (GMU) in Colorado, USA, 2004–2014.

woodlands dominated by Ponderosa pine (*Pinus ponderosa*) at mid-elevation to the spruce-fir (Engelmann spruce [*Picea engelmannii*], subalpine fir [*Abies lasiocarpa*], and Douglas-fir [*Pseudotsuga menziesii*]) and aspen (*Populus tremuloides*) forests at the highest elevations of about 3,000 m. Mid-elevation forests were interspersed with oak-serviceberry (Gambel oak [*Quercus gambelii*] and Saskatoon serviceberry [*Amelanchier alnifolia*]) shrublands. Expansive sagebrush-steppe (sagebrush [*Artemisia* spp.] and -grass) meadows and basins occupied mid-to-high-elevations, especially in the south-central portion of the area.

Weather was somewhat similar during the 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 of 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 (–3.4°C, range = –23.3–12.8) and average July temperature (19.4°C, range = 2.2–33.9).

The prey community available to puma on the UPSA was diverse, and included wild and domestic animals. Mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) were common on the Uncompahgre Plateau and surrounding areas. 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 consisted 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 and domestic sheep 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 and western fringes of the area. Other animals kept by people included alpacas, llamas, goats, and pigs. There were 5 recorded incidents of puma predation on these animals during this study, with each incident involving 1–4 animals (CPW, Game Damage Program, unpublished data).

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 (CPW, unpublished data). Based on the
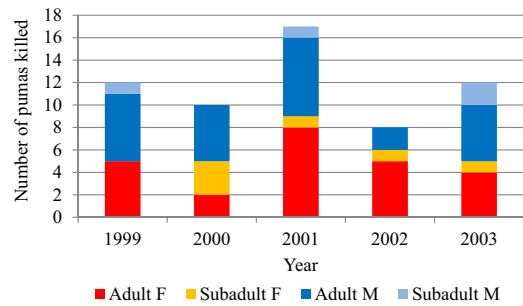
Figure 2. Number of adult and subadult female (F) and male (M) pumas reported killed by hunters during 1999–2003 on the Uncompahgre Plateau Study Area prior to our study, Colorado, USA.

records of the sex and age classes of the animals killed, 41% were classified as adult females; the rest were adult males and subadults of both sexes (Fig. 2). 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.

METHODS

Puma Research and Management in Colorado

We designed this 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. Sizes of DAUs range from 4,048–21,054 km^2 ($\bar{x}$ = 9,282 km^2). The 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 were not discrete puma populations because we expected the animals to move across administrative boundaries given that home ranges of adults in North America vary in size from about 50–700 km^2 (Logan and Sweanor 2010) and 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).

Colorado Parks and Wildlife managers attempt to manipulate puma abundance with hunting at the DAU scale. Within each DAU, they apply assumptions and judgments on density, sex and age structure, population growth rates, and impacts of hunting and other causes of mortality. Each GMU within a DAU is allocated a harvest quota (i.e., harvest limit) to spatially distribute harvest to achieve 1 of 2 desired DAU-wide population states: 1) a stable or increasing population to provide hunting opportunity and species conservation, and 2) a declining or low-phase population with hunting used to reduce puma conflicts with livestock, big game ungulates, and human safety while also providing hunting opportunity. Management plans for DAUs identify mortality rates of independent pumas expected to achieve the desired population states (i.e., 8–15% for stable or increasing, ≥16% for declining).

Puma hunting seasons began in mid-November and ended in March, at latest. Quotas were not sex-specific. Successful hunters were required to report their kills to CPW within 48 hours

of harvest and present carcasses for inspection within 5 days of harvest. 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

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 movements in relation to study area boundaries and emigration. We handled all animals 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 and the Animal Care and Use Committee of the American Society of Mammalogists 2016). We marked captured pumas with a telemetry collar, ear-tag (Allflex USA, Dallas, TX, USA), and tattoo. An identification number tattooed in at least 1 pinna was permanent and could not be lost unless the pinna was detached.

We captured pumas using trained dogs, cage traps, and by hand (for small cubs). Pumas captured with dogs usually climbed trees to take refuge. We anaesthetized adults and subadults captured for the first time or requiring a change in telemetry collar with Telazol (tiletamine hydrochloride-zolazepam hydrochloride) dosed at 5 mg/kg estimated body mass. We delivered the drug into the caudal thigh or shoulder muscles via a Pneu-Dart® shot from a carbon dioxide-powered pistol (Pneu-Dart X-Caliber; Pneu-Dart, Williamsburg, PA, USA) or by a syringe at the end of an extendable pole. We deployed a 3-m by 3-m square nylon net beneath the puma to catch it in case it fell. We immediately restrained individuals that fell into the net 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 animal and lowered it 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 its tracks until we found it sedated on the ground. To secure the animal, we covered its head, tethered it legs, and then monitored its vital signs. We considered normal signs to be pulse = 70–80 bpm, respiration = 20 bpm, a capillary refill time of ≤2 seconds, and rectal temperature = 38.3°C average (range = 35–40°C; Kreeger et al. 1999). We recorded the sex and dental characteristics of each puma we handled and measurements of each adult and subadult animal, including the length and width of plantar pads (mm measured with calipers), total length, tail length, chest girth, hind foot lengths (cm measured with a steel tape), and weight (kg measured with a spring scale). When a treed puma could not be safely immobilized and handled, we simply recorded the individual's sex, life stage, association with other individuals (e.g., mother, siblings), and location prior to leaving it.

Cage traps captured adults, subadults, and large cubs (Bauer et al. 2005, Sweanor et al. 2008). We lured animals to traps using road-killed or puma-killed ungulates. We set a cage trap only if a target animal (i.e., an unmarked, required a collar change) scavenged on the lure. We continuously monitored a set cage trap from about 0.5–1 km distance by using very high frequency (VHF) beacons on the cage. This allowed us to respond to a captured puma in ≤30 minutes. We sedated them 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 as determined by radio-telemetry. We captured cubs ≤10 weeks old 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 marked each cub and recorded data on litter size. Afterwards, we immediately returned the cubs to the exact nurseries and vacated the area (Logan and Sweanor 2001).

We fitted captured adult and subadult pumas with either global positioning system (GPS; Lotek GPS 4400S) or VHF (Lotek LMRT-3; Lotek Wireless, Newmarket, Ontario, Canada) collars, each weighing about 400 g and 300 g, respectively. Budget constraints limited the number of GPS collars available annually; therefore, we fitted those collars primarily to adult pumas of both sexes. We fitted other adults and subadults with the VHF collars.

We attempted to collar all cubs in each observed litter of nurslings with a small VHF transmitter (model 080; Telonics, 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. We fitted cubs weighing ≥7 kg with a larger expandable collar weighing 90 g (model 210; Telonics) that also could expand to 54 cm circumference. We fitted cubs approaching the age of independence (11–14 months old) with Lotek LMRT-3 VHF collars each with a leather expansion link that added 10–14 cm to the collar circumference to accommodate an adult neck size.

We initially estimated the ages of adult pumas by the gum-line recession method (Laundré et al. 2000) and later with dental characteristics of known-age animals (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 individuals into 2-year age increments to examine age structures and to back-age certain adults into previous winter counts. We estimated ages of subadults and cubs initially based on dental and physical characteristics of known-age pumas from New Mexico (K. A. Logan, Colorado Parks and Wildlife, unpublished data) and later from known-age animals 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 adults and subadults in winter to gather data on harvest-age animals 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 affected 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 to avoid interfering 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 animals. When we followed fresh 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 animals and toward finding non-collared ones.

We monitored radio-collared pumas year-round. We programmed GPS collars 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. The VHF and GPS collars had mortality modes set to alert researchers when animals were immobile for 3 hours and 24 hours, respectively, so that we could examine dead pumas. 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 recurring movements to farther distances that returned to focal locations (Logan and Sweanor 2001).

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, animals 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 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 animals using the UPSA in TY1. We modeled this estimate from 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 animals for TY4. The model projected 44 pumas, so we adjusted the harvest quota down to 5, an expected 11% target harvest in TY4, to examine the effect of a reduced harvest on abundance. We also applied the quota of 5 pumas in TY5 (Table S1, available online in Supporting Information).

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).

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 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 permit from the CPW Service Center in Montrose, Colorado. Each permit allowed the 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 season. Each hunter also received a voluntary survey with their hunting permit and a stamped return envelope. We asked hunters to complete the survey as soon as possible for each 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 that included 1) permit holders that actually hunted on the UPSA; 2) number of days each hunted on the UPSA; 3) the sex of puma (we provided hunters with male and female track measurements) that made the first set of tracks <1 day old that a hunter encountered on the UPSA (representing the first theoretically catchable independent puma); 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 animal (i.e., collar, ear-tags) influenced a hunter's decision to harvest it; 7) if the hunter used dogs; and 8) self-identification as a selective or non-selective hunter. On this last point, we provided 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, and thus is deciding not to kill certain pumas. A non-selective hunter is one that intends to harvest whatever legal puma is first encountered or caught, with no preference for sex or size.

Our research personnel visually examined each puma harvested on the UPSA and officially marked it with a metal, numbered tag to indicate legal possession by the hunter, consistent with Colorado

hunting regulations. At the time of carcass check-in, hunters also completed a CPW mandatory harvest form, which included the puma's sex, age estimate, date of kill, and kill-site location.

Analysis

Abundance and growth rates.—The parameter of interest to wildlife managers was the abundance of independent pumas (i.e., adults and subadults) each winter coinciding with the hunting season in Colorado. Initially, we obtained an index of abundance of independent pumas that used the UPSA based on counts of animals we detected from November through March (i.e., winter counts) from RY4–TY3 (Table S1). We used this information for setting the hunting quotas in the treatment period. Winter puma counts consisted of the sum total of all individuals, including known marked, non-marked we captured but could not safely handle, and non-marked harvested on the UPSA. In addition, our counts included other individuals of unknown identity detected by their tracks as recorded by our capture teams on the study area. We concluded that individuals were unique if their track characteristics fit these criteria: 1) did not match known movements and locations of radio-collared pumas, 2) exhibited measurements that did not match those of individuals we subsequently captured, and 3) different counts of cub tracks with mother's tracks (e.g., mother's tracks associated with tracks indicating 1, 2, or 3 cubs would differentiate mothers). We used hind-foot plantar pad inside width measurements to distinguish sex (≥ 52 mm classified as male, ≤ 50 mm classified as female [measured with a steel ruler]).

After we compiled all our data on winter capture efforts, observed mortalities, and fates of pumas with non-functional collars, 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 before any individuals were removed from the population from RY2–TY5:

$$\hat{N}_c = [(n_1 + 1)(n_2 + 1)/(m_2 + 1)]$$
$$- 1 \quad \text{(Pollock et al. 1990:equation 2.2)}.$$

This approach also provided estimates of variance:

$$\text{var } \hat{N}_c = (n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)/(m_2 + 1)^2$$
$$\times (m_2 + 2) \quad \text{(Pollock et al. 1990:equation 2.3)}$$

and precision with 95% confidence intervals:

$$\hat{N}_c \pm 1.96 \, (\text{var } \hat{N}_c)^{0.5} \quad \text{(Pollock et al. 1990:11)}.$$

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. We treated each 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 individuals with home ranges that overlapped the border of the UPSA. Detections consisted of marked independent pumas recaptured by hunters, previously marked animals we recaptured during our winter capture operations, and radio-collared individuals we detected by following tracks toward radio-signals during our ground-capture operations. We counted radio-collared adults in the n_1 data with home ranges that overlapped the UPSA and adjacent areas as detected in the m_2 data if they were harvested on a portion of their home range off the UPSA. We counted adult pumas with failed radio-collars that had previously established home ranges on the UPSA 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. If any of these individuals had temporarily emigrated from the UPSA when they went undetected in any year, then the actual number of independent animals using the UPSA would be somewhat lower. 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) beginning 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); we counted those individuals in the n_2 data. If any of these individuals were actually absent in any of those years, again, the actual number of independent animals using the UPSA would be lower. We used the change in the LP $\hat{N}_c$ estimates and the 95% confidence intervals as a gauge of changes in the population 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, Kendall 1999). 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 prone to errors of underestimation. We were unable to use a robust design capture-recapture model (Schwarz and Stobo 1997) because the sampling intervals were inadequate for that method. We attempted to use the Jolly-Seber approach to estimation of abundance (Jolly 1965, Seber 1965) in Program MARK (White and Burnham 1999), but models would not converge on a solution for the maximum likelihood. Other approaches to estimation of density rather than abundance (e.g., Efford 2004, Ivan et al. 2013) also assume closed populations and thus would invoke similar biases to our method.

We estimated the finite rate of change in abundance (λ) and its 95% confidence interval each year during the reference and treatment periods, RY2–TY5, to interpret changes in abundance without and with the hunting treatment (Fryxell et al. 2014). To calculate λ, we drew 10,000 samples using R statistical software (version 3.1.1; R Core Team 2018) 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 1 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% confidence interval.

Sex and age structure.—We quantified the sex and age structure of independent pumas on the UPSA each winter RY1–TY5 based on the animals that were captured and the LP estimates. We also used counts of cubs we captured and counts of non-captured cubs we detected from tracks associated with mothers. We graphed the sex and age structure annually for independent pumas that we physically examined (i.e., captured and handled or harvested) by sorting individuals into 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.

Mortality.—We estimated cause-specific mortality rates of independent pumas at 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 animals at this larger scale for 2 reasons: First, managers considered puma population segments at a DAU scale (i.e., population scale) for setting broad population state objectives. Second, we recognized that the local UPSA population was open and could be affected by fates of pumas ranging on the UPSA and adjacent GMUs.

The smaller scale represented 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 animals using a GMU that died within the boundaries of the GMU to denote how managers may view mortality rates in units on which they limit the harvest and that are small relative to the population. 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. These estimates were biased because the use of LP estimates in an open population can itself be biased, specifically in systems with non-random movement in and out of the study area (Seber 1982, Kendall 1999). Furthermore, the numerator only included animals that died within the UPSA boundaries, but the denominator included animals ranging on and off the UPSA; thus, the estimate was biased low. 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 UPSA plus independent pumas with overlapping home ranges that died on adjacent GMUs divided by the LP $\hat{N}_c$ estimate of independent pumas using the UPSA). This metric could partially mitigate the biases in the first estimate but could not account for any non-marked

pumas estimated in the denominator that might have had home ranges overlapping the UPSA and 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 animals were reported to have died to calculate annual rates of agent-specific mortality. We used simple quotients with the numerator being the number of marked individuals that died each biological year (i.e., Nov–Oct) and the denominator 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 confidence intervals 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 estimated the proportions of litters subject to infanticide in the reference and treatment periods by calculating the binomial proportions and Clopper-Pearson exact 95% confidence intervals by using the PROC FREQ procedure in SAS (version 9.3; SAS Institute, Cary, NC, USA).

Philopatry, dispersal, and emigration.—We defined pumas born on the study area as philopatric if any of their adult stage locations occurred within the 100% minimum convex polygon (MCP) of their mother's cumulative locations (Minimum Bounding Geometry tool, Convex Hull option, ArcGIS version 10.2; Esri, Redlands, CA, USA). We considered individuals born on the study area to have dispersed if none of their adult locations occurred within their mother's MCP. We measured dispersal distances in kilometers using the planar measuring tool in Arcmap 10.2 (Esri) 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 age at independence (i.e., at the first observed date of separation from mothers without returning) and dispersal of previously radio-collared cubs (i.e., at date of first observed location outside of its mother's MCP without returning), and reported medians, averages, and 95% confidence intervals. We considered pumas that moved completely outside the boundaries of the UPSA to be emigrants. Those included some young independent animals that we 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-population-scale emigration rates we estimated when analyzing puma mortality because of the shorter movement distance needed for individuals to exit the UPSA.

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 hunting seasons began) through the next October to encompass complete hunting seasons. We estimated survival rates of subadults and cubs 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) to model survival rates with a candidate set of models that might explain variation in survival (below).

We defined adult pumas 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 value was close to the estimated average age of 29 months of first conception for a sample of 14 females in this study (see reproduction results). Furthermore, because our capture efforts for independent pumas were focused during November to April, the youngest animals in the adult stage in November generally could have been 26–32 months old, assuming they were born within the monthly distribution of 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).

We examined adult survival from data on radio-collared pumas. We converted radio-location records for each adult 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 adults started on the day of capture or the beginning of RY2 (i.e., 1 Nov 2005) for surviving pumas that we 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. We used known death dates for individuals killed and reported by hunters, those killed for depredation control, and for some vehicle strikes. For individuals that died of other causes, we assigned death dates to those with GPS collars based on the first day that GPS locations indicated that they were immobile. For VHF-collared pumas, we estimated dates as the mid-point of the span of days in which we estimated the animal to have died based on detection of radio-collar mortality signals and carcass decomposition. We categorized causes of death 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). We estimated subadult survival for all known radio-collared, ear-tagged, and tattooed pumas with known fates. Individuals entered the subadult stage under 2 conditions: 1) after they were known to be independent from their mother based on radio-telemetry, 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 ($\bar{x} = 13.7$ months) for a sample of 15 pumas at known age of independence in this study (see results). Because we did not know exactly when all of the pumas in this life stage became independent, some of them may have been dependent cubs for ≥13 months. Encounter histories started when marked pumas entered the life stage and on the first day of capture for subadults caught and marked for the first time. We converted individual radio-telemetry records to monthly encounter histories. We assigned death dates as for adults.

We estimated cub survival 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 animals. The large majority (i.e., 85 of 118) of cubs in this data set were initially radio-collared as 1–2-month-old nurslings. We entered older cubs we collared in the analysis because we converted individual radio-telemetry 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 and recorded known dates of occurrence. If dates of death were not observed, we used the mid-point of the span of days in which the puma was estimated to have died based on the radio-telemetry 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 vs. treatment) effect would support an inference that hunting mortality was an important factor explaining the variation in puma survival. However, if models lacking the period result 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 outcome. 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 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 survival for all 3 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 $\Delta AIC_c < 2$ as having the most support. We report survival estimates for the top model and other supported models. For adults, we used the monthly

survival rates generated in MARK and converted them to annual rates (i.e., $S_{monthly}$12) with 95% confidence intervals. We used the delta method (Dorfman 1938) to calculate confidence intervals for annual survival rates. Likewise, we used monthly survival rates in MARK for subadults and converted them to life stage survival rates with 95% confidence intervals.

For cub survival, the assumption that each radio-collared individual was an independent random sample (i.e., distribution of mortalities among litters is random) may be violated because we often collared 2–3 cubs 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 and the data are 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 1,000 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% confidence intervals.

Reproduction.—Females with GPS and VHF collars provided data on parturition (date), gestation (days), litter size (number), sex of cubs observed in nurseries, birth intervals (months), and age at first breeding (months). We verified reproduction 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 their first litters that we observed. We assigned a non-productive status to females with nipples that were tiny and pink or white in color indicating no previous suckling. We reported mean age at first breeding, range, and 95% confidence intervals. We estimated gestation lengths 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 means with 95% confidence intervals.

We estimated parturition rate, defined as the proportion of adult females giving birth each year, from RY2 through TY5 when $\geq$12 adult females occurred in annual samples ($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, we modeled mean period parturition rate by using the generalized linear mixed model procedure with the binomial distribution and logit link (PROC GLIMMIX) in

SAS 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 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 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. We used a normal distribution error structure 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% confidence intervals by using the PROC FREQ procedure in SAS. We made inferences on period effects on parturition rate (on the logit scale), birth interval, litter size, and proportions of the sexes in litters by examining the 95% confidence intervals on the differences of the estimates for each period by using the delta method (Seber 1982).

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

RESULTS

Puma Capture

From 2 December 2004 to 30 October 2014, we captured as many as 256 pumas a total of 440 times on the UPSA. We considered about 30 individuals to be captured with dogs but we did not handle or mark them at that time because of their dangerous positions in trees or on cliffs. Of those, 11 were in the reference period, of which 6 were associated with marked family members (i.e., mothers or siblings). In the treatment period, we did not handle 19 captured pumas, 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 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 adults or subadults died from capture procedures. One cub was killed by our tracking dogs. Three cubs died as a result of premature expansions of the radio-collars: 1 nursling starved because the transmitter was caught in its mouth and 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 animals 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 of marked individuals in the life stage classes (268) is greater than the total of uniquely marked pumas. By the end of the study, we accounted for the fates (i.e., either survived or died) of all of the radio-collared adults, including those with failed radio-collars, except for 1 female and 1 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. 3A). One subadult male was harvested in a GMU adjacent to the UPSA. Over twice as many adults died of natural causes (i.e., intraspecific killing, other causes) than adults that died from human causes (i.e., vehicle strikes, depredation control). Intraspecific killing was the major single cause of death for adults, with 3 times as many females than males. A majority (i.e., 6 of 10) of the independent pumas that died were adult females, with the remainder composed of adult males and subadults. Two subadult female deaths occurred, 1 each from a vehicle strike and trampling by an elk.

In the treatment period, human-causes, hunting in particular, were the most important sources of death for marked adults and subadults, comprising 65% and 100% of adult female and male mortalities, respectively, and 75% of both subadult female and male mortalities (Fig. 3B). Adult females in particular (i.e., 35% of their deaths), and to a lesser extent subadults, 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 that cause during our entire study.
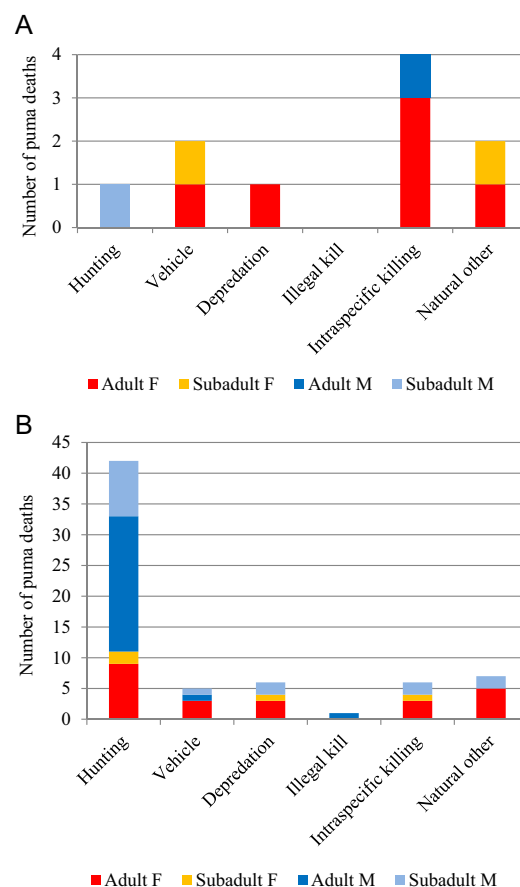
Figure 3. Proximate causes of death in marked adult and subadult female (F) and male (M) pumas during the reference period (A) and the treatment period (B), 2004–2014, Uncompahgre Plateau Study Area Colorado, USA.

Hunting Treatment and Other Mortality

A harvest quota of 8 pumas on the UPSA during TY1–TY3 resulted in 9 animals harvested in TY1 and 8 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, UPSA-specific harvest rates averaged 13%. Males 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 average estimated age of all the pumas harvested on

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 | Adult | | Subadult | | | Total number of |
year	Female	Male	Female	Male	Quota	pumas harvested
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 from reference years 2–5 (RY2–RY5) and treatment years 1–5 (TY1–TY5), 2005–2014, Uncompahgre Plateau Study Area (UPSA), Colorado, USA.

Study winter[a]	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] We treated each entire capture and hunting season (Nov–Mar) as a sampling period.
[b] Number of marked independent pumas expected to be in the UPSA at the start of the sampling period (i.e., Nov).
[c] Number of independent pumas physically captured, detected by radio-telemetry, and back-aged into the sampling period.
[d] Number of independent pumas detected during the sampling period in the n_2 sample that were previously marked.
[e] Pre-harvest abundance in November.
[f] 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 Game Management Units (in parentheses) expressed as a proportion of Lincoln-Petersen abundance estimates ($\hat{N}_c$) during hunting seasons from treatment year 1 (TY1) to treatment year 5 (TY5), 2009–2014, Colorado, USA.
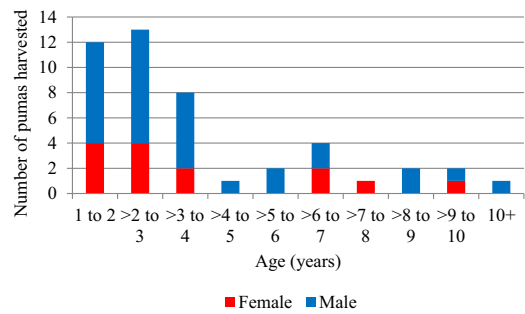
Treatment year	Puma harvest rate	Total human-caused puma mortality rate	Total puma mortality rate
TY1	0.16 (0.25)	0.16 (0.25)	0.16 (0.25)
TY2	0.14 (0.16)	0.18 (0.20)	0.18 (0.20)
TY3	0.18 (0.23)	0.18 (0.23)	0.23 (0.27)
TY4	0.12 (0.19)	0.12 (0.19)	0.14 (0.21)
TY5	0.14	0.14	0.16

Figure 4. The age structure of pumas harvested on the Uncompahgre Plateau Study Area (UPSA) and with home ranges overlapping the UPSA that were harvested on adjacent Game Management Units, 2009–2014, Colorado, USA.

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%.

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 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 average estimated 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. 4).

All marked adults that died from hunting (9 females, 22 males) and depredation control (3 females) were detected by, or reported to, wildlife managers. However, 18 adult deaths, including 15 natural (14 females, 1 male), an illegal kill (1 male), and 2 (both females) of the 4 vehicle strikes (3 females, 1 male) were not detected by wildlife managers but instead by our radio-telemetry monitoring. All marked subadult 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 deaths (2 females, 4 males) due to natural causes.

the UPSA during the treatment period was 3.5 years (range = 1.1–9.5).

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 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

Table 4. 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 Game Management Units (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

Table 5. Mortality causes and number and percentage of deaths by sex and total by period of radio-collared puma cubs during the reference ($n = 28$ female, 27 male) and treatment ($n = 27$ female, 36 male) periods, 2004–2014, Uncompahgre Plateau Study Area, Colorado, USA.

Study period	Mortality cause	Female deaths (%)	Male deaths (%)	Total deaths (%)
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)

Figure 5. 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.
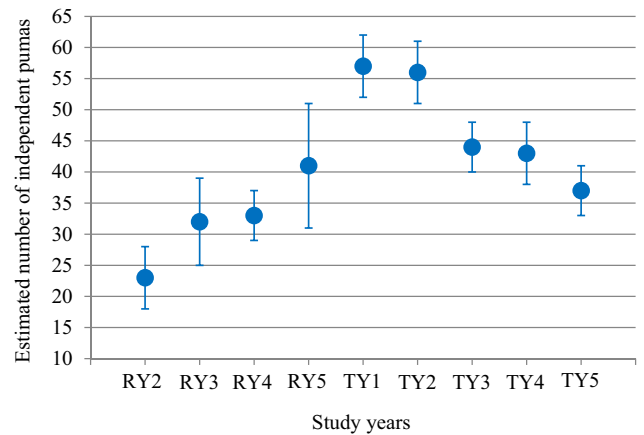
Of 55 radio-collared cubs (28 females, 27 males) monitored in the reference period, 18 died (Table 5). Of those, 72% died when ≤5 months old. Natural causes dominated deaths of cubs (94.4%), of which infanticide was the greatest single cause (72.2%). One cub was killed by a vehicle strike. Four non-collared 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 mortality during the treatment period. Infanticide deaths declined from 72.2% to 29.6%, and human-caused deaths increased from 5.6% to 44.4% from the reference period to the treatment period. In addition, we observed mortality in 3 litters of non-collared cubs: 2 litters (1 with 2 cubs and 1 with ≥1 cub) died of infanticide, and the third litter (with ≥1 cub) died because of 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% confidence intervals (–0.04–0.32) on the difference included zero.

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. 5) 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 showed 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. 5). In total, estimates of independent pumas that ranged on the UPSA declined 35% by TY5 following 4 hunting seasons (TY1–TY4) in which annual harvest rates averaged 15%. For the population declines measured by TY3 and TY5 where the TY1 95% confidence interval on the estimate does not overlap with the interval of TY3, the first indicated decline, and the interval for TY5, the last year, the total human-caused mortality rates on the UPSA averaged 17% and 16%, respectively. Likewise, 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
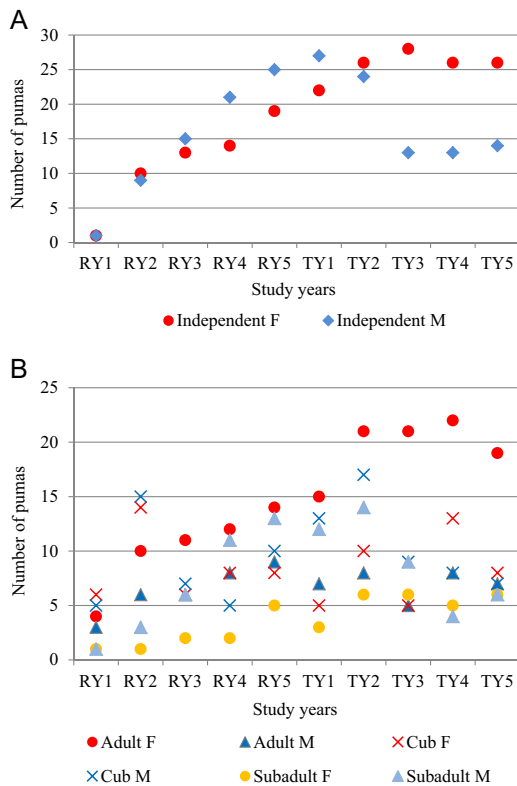
Table 6. Estimated finite growth rates (λ) and lower and upper 95% confidence limits (LCL, UCL) of independent puma abundance, reference years 2–5 (RY2–RY5) and treatment years 1–5 (TY1–TY5), 2005–2014, based on Lincoln-Petersen estimates ($\hat{N}_c$) of independent pumas in winter, Uncompahgre Plateau Study Area, Colorado, USA.

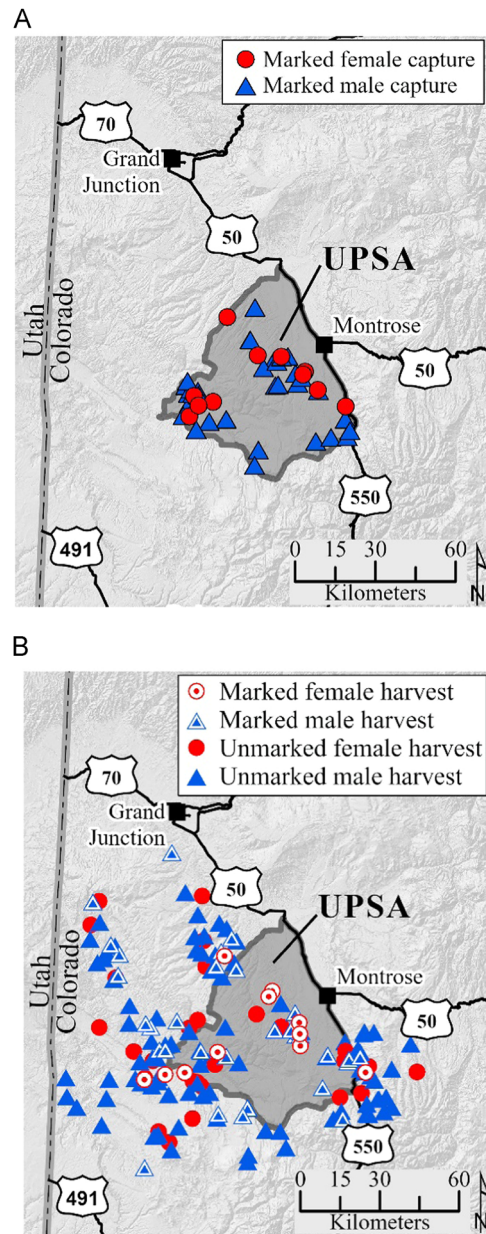|	λ		
Interval	Median	95% LCL	95% UCL
RY2–RY3	1.39	1.01	1.94
RY3–RY4	1.04	0.83	1.34
RY4–RY5	1.25	0.94	1.58
RY5–TY1	1.39	1.10	1.82
TY1–TY2	0.98	0.87	1.12
TY2–TY3	0.79	0.70	0.88
TY3–TY4	0.98	0.85	1.13
TY4–TY5	0.87	0.74	1.02

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.

Our multinomial analysis of fates of marked independent pumas at the population scale included 19–44 individuals annually from RY2–RY5 and 39–50 annually TY1–TY5 (Fig. 6A). 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. 7). Only 1 of the marked independent pumas with known fates was harvested during the reference period, a subadult male killed in a GMU adjacent to the UPSA in RY5. In contrast, annual harvest rates in the treatment period ranged from 13–27% (Table 7). Population-level harvest rates for years TY1–TY4 averaged 22% (Table 7), and preceded the 35% reduction in the estimated abundance of independent pumas on the UPSA by TY5. 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. Average annual natural mortality rates

Figure 7. 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.

were low in both the reference and the treatment periods (5%, 6%, respectively). Total annual mortality rates averaged 8% in the reference period and increased to 31% in the treatment period. The average annual population-scale emigration rate (i.e., from the UPSA and adjacent GMUs) was similar in the reference and treatment periods (8%, 4%, respectively).

Sex and Age Structure

The sex and age structure on the UPSA in winter, based on LP estimates of adult females, males, and subadults 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

Figure 6. Numbers of marked independent (i.e., adults and subadults) female (F) and male (M) pumas for multinomial analysis of cause-specific mortality rates (A), and adult, subadult, and cub pumas for survival rate estimates (B), reference year 1 to treatment year 5 (RY1–TY5), 2004–2014, on the Uncompahgre Plateau Study Area and bordering Game Management Units, Colorado, USA.

Table 7. Population-scale estimated puma agent-specific mortality rates and emigration rates (with 95% CIs) 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.

pumas was lowest. As the abundance of adults 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. 8) 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 of which there were over twice as many females as males (Fig. 8). In the first 2 years of the reference period, adults >5 years old were few (Fig. 8). The number of pumas >5 years old increased, however, during RY3 to the beginning of TY1 as the population on the UPSA increased.

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. 8). Pumas 1–5 years old comprised 66% of the independent animals; the other 34% were adult females and males >5 years old (Fig. 8). In TY1, adult males >5 years old comprised 43% of that segment of the population. Estimated winter

Table 8. Lincoln-Petersen winter estimates and 95% confidence intervals of adult female, adult male, and subadult (sexes combined) pumas, and counts of cubs (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[a]	Adult females	95% CI	Adult males	95% CI	Subadults	95% CI	Cubs[b]
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 because of rounding errors for RY4, RY5, TY3, and TY4.
[b] Includes cubs observed with mothers and cubs counted from tracks associated with mothers.

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. 8D). 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 (21) as males (23) 1–2 years old throughout the treatment period.

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 (Fig. 8C).

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.

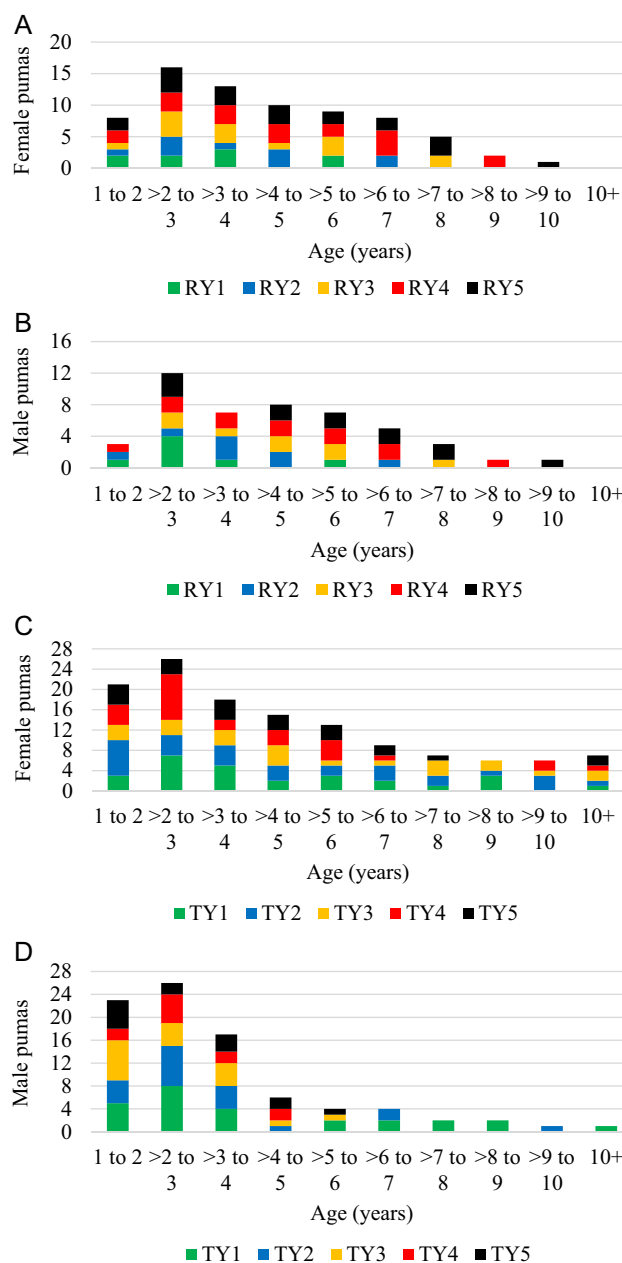## Philopatry, Dispersal, and Emigration

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 ($\bar{x}$ = 13.7 months, range = 9–16). Ten pumas (8 males, 2 females) dispersed from natal areas at a median age of 14.5 months ($\bar{x}$ = 15.5 months, range = 10–22) and during April to October. Seven of those (5 males, 2 females) dispersed from natal areas

Figure 8. 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 are presented in panels A and B, respectively, for reference period years (RY1–RY5). Females and males are presented in panels C and D, respectively, for treatment period years (TY1–TY5).

before their first winter in the subadult stage, and all except for 1 female emigrated from the UPSA.

Six marked pumas born on the study area that survived to adult ages exhibited philopatry. Five females established adult home ranges overlapping those of 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 his 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 radio-collar 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 km 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 (27%; 9 males, 1 female) were known to have emigrated from the UPSA. Similarly, of 36 cubs surviving to subadult stage in the treatment period, at least 9 (25%; 8 males, 1 female) 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. 9). Four females and 24 males emigrated entirely from UPSA. Females dispersed an average of 30.7 km (95% CI = 23.2–38.2,
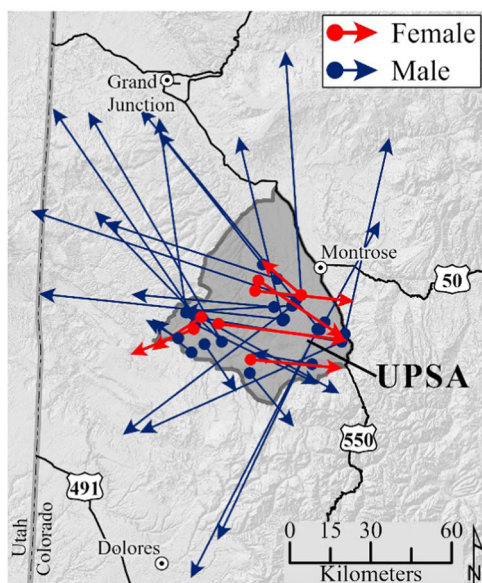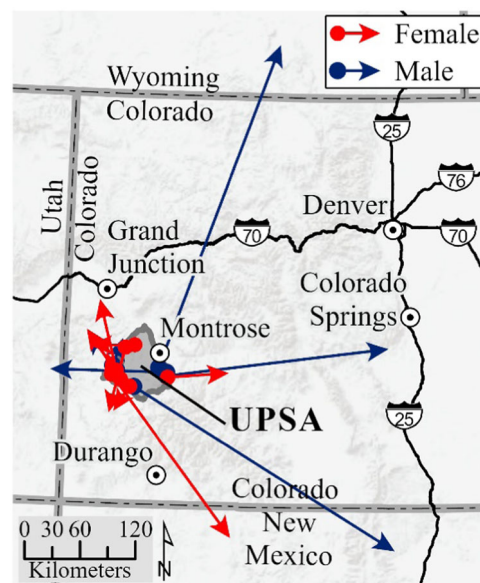
Figure 9. Pumas born, captured, and marked on the Uncompahgre Plateau Study Area (UPSA) Colorado, USA, 2004–2014, that later dispersed from their natal areas after separation from mothers. End points of their movements indicated by the ends of the arrows are to the last known locations.

Figure 10. 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.

range = 18.7–46.8). We determined dispersal endpoints for females when they were 17–44 months old ($\bar{x} = 26.7$, 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). We determined dispersal endpoints for males when they were 17–65 months old ($\bar{x} = 33.1$, 95% CI = 27.8–38.3).

We obtained data on 14 other independent pumas (8 females, 6 males) with unknown origins that were initially captured and marked on the UPSA but subsequently emigrated (Fig. 10). 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 ($\bar{x} = 33$, 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 ($\bar{x} = 39$, 95% CI = 29–49) when we determined their endpoints. Pumas from this group made the farthest movements; 1 female and 1 male moved to northern New Mexico, 1 male moved to the eastern slope of the Rocky Mountains in Colorado, and 1 male moved to southern Wyoming.

Survival

Adults.—The adult 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. 6B). Survival modeling resulted in 2 closely ranked models ($\Delta AIC_c < 2$) that accounted for 89% of the model weights. The top-ranked model indicated a period effect interacting with sex

(Table S2, available online in Supporting Information). Adult male annual survival was over 2 times higher in the reference period (0.96) than in the treatment period (0.40; Table 9). The estimate for annual adult female survival was also higher in the reference period (0.86) than in the treatment period (0.74). 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. 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 ($\Delta AIC_c > 4$).

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.

Table 9. Top-ranking survival models (difference in corrected Akaike's Information Criterion [ΔAIC_c] < 2) for adult and subadult pumas, and estimated adult annual and subadult stage survival rates with 95% confidence intervals, 2005–2014, Uncompahgre Plateau, Colorado, USA.

Life stage	Model[a]	Sex	Reference period survival (95% CI)	Treatment period survival (95% CI)
Adult[b]	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[c]	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] Period = reference (no hunting) vs. treatment (hunting allowed). M = male. F = female.
[b] Sample sizes of adult pumas included 11 males and 21 females in the reference period and 22 males and 39 females in the treatment period.
[c] Sample sizes of subadult pumas included 14 males and 8 females in the reference period and 34 males and 19 females in the treatment period.

The number of subadult females and males monitored annually ranged from 1–6, and 1–14, respectively (Fig. 6B). Survival modeling resulted in 2 closely ranked models ($\Delta AIC_c < 2$) that accounted for 77% of the model weights (Table S3, available online in Supporting Information). The top-ranked model indicated period as an important factor explaining male survival and constant female survival. Subadult male survival was 2 times higher in the reference period (0.92) than in the treatment period (0.43). Subadult female survival was 0.68 over the 2 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. Subadult male survival varied in the 2 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 ($\Delta AIC_c > 2$).

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 females and males monitored annually ranged from 5–14, and 5–17, respectively (Fig. 6B). 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 from 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 from 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 a $\Delta QAIC_c < 2$; all 4 supported models contained the covariate for mother status alive or dead (i.e., mother status) and accounted for 78% of the model weights (Table S4, available online in Supporting Information). 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 mother status alone had 2.5 times the support of the second-ranked model, sex + mother status, and 2.7 times the support of the third- and fourth-ranked models, period + mother status and sex × period + mother status, respectively. In the top model, the survival estimate of cubs with living mothers (0.51) was over 3 times higher than of cubs whose mothers died (0.14; Table 10). With sex and mother status as main effects, survival estimates of male and female cubs (0.54 and 0.49, respectively) with living mothers were 3 to 4 times higher than for cubs of those sexes (0.16 and 0.12, respectively) with mothers that died. With period and mother status as main effects, 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 mother status as a main effect 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 and 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 and 0.19, respectively) with mothers that died. There was no support for period alone explaining variation in cub survival ($\Delta QAIC_c = 5.8$).

Reproduction

Adult females 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. 11).

Table 10. Top-ranking survival models (difference in corrected quasi-Akaike's Information Criterion [$\Delta QAIC_c$] < 2) for puma cubs monitored in the reference (27 males, 28 females) and treatment (36 males, 27 females) periods, and the estimated stage survival rates with 95% confidence intervals, 2005–2014, Uncompahgre Plateau, Colorado, USA.

Model[a]	Covariates		Survival (95% CI)
Mother status	Mother alive		0.51 (0.35–0.66)
	Mother dead		0.14 (0.03–0.34)
Sex + mother status	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 + mother status	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 + mother status	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)

[a] Mother status = mother was alive or dead when individual cubs were dependent. Period = reference (no hunting) vs. treatment (hunting allowed).
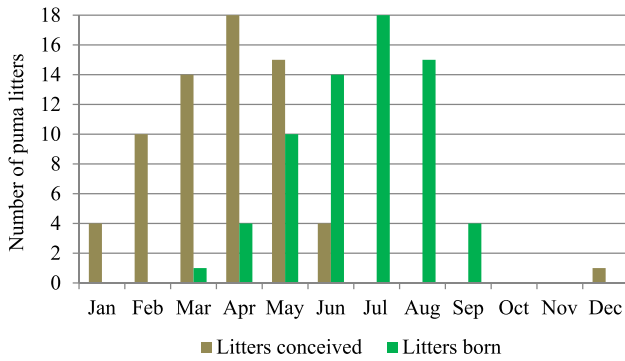
Figure 11. Monthly puma conception and birth frequency from 19 May 2005 to 30 September 2014 ($n = 66$ litters of 33 females). We examined 60 litters at nurseries when cubs were 25–45 days old; we confirmed 4 litters by tracks of ≥ 1 cubs following radio-collared mothers and 2 litters by remains of cubs of 2 radio-collared mothers when cubs were ≤ 45 days old, Uncompahgre Plateau, Colorado, USA.

We estimated minimum and maximum gestation for 17 litters of 13 females. Gestation length medians were 91–92 days and averages were 90.4–91.8 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. 11).

The 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 a 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% confidence intervals on the differences of the estimates for each period for all parameters included zero.

Puma Hunters

The number of people requesting a permit to hunt on the UPSA each 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 the people 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 greatest number of hunters participated in TY1. The lowest numbers of hunters were in TY4 and TY5 when the quota was reduced to 5 pumas. Hunters on the UPSA generally used dogs to hunt pumas, yet 1–4 individuals (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 an animal. 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.

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 person hunted on UPSA ranged from 1–14, and the median number of days for each year was either 1 or 2. Hunter effort to harvest a puma ranged from 1–6 days and medians ranged from 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 (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 ranged from

Table 11. Puma reproduction parameter estimates and 95% confidence intervals 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] We made inferences on period effects on these parameters 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.

Treatment year[a]	Number of hunters that requested permit	Number of hunters that responded to survey	Percent of hunters that returned survey	Number of hunters that indicated they hunted on UPSA	Estimated number of 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.

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	Number of days hunted on UPSA (range, median, n)	Number of days to fill the quota	Number of 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

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 females 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 seasons.

Hunters self-identified as selective 84–97% of the time and the sex ratio of independent pumas killed (2.2 males:1 female)

reflected selection toward males (Table 14). Hunters harvested more males than females, even though they reported encountering more fresh female tracks in 3 of 4 seasons that we asked this survey question. 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.

DISCUSSION

Overarching Demographic Effects of Hunting

We found that annual harvest rates of independent pumas averaging 22% at the larger population scale and 15% at the UPSA scale over 4 years resulted in a 35% decline in their abundance on the main study area. As noted previously, however, the 15% UPSA-scale average harvest rate is biased low

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

| Treatment year	Sex ratio of first 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 first 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] Not addressed in hunter survey in TY1.

because of the mis-match of the harvest limited on the UPSA (the numerator) relative to the number of independent pumas using this and adjacent areas (the denominator). Moreover, if we committed any errors by counting adults with failed radio-collars and others we back-aged to ≥2 years old in LP parameters, the actual UPSA-scale harvest rate would be higher. Hunting deaths were largely additive as indicated by a decline in survival and abundance and no reduction in other causes of mortality. Also hunting mortality was not fully compensated by reproduction and recruitment. Recruitment of young pumas did not compensate for losses of adult males and only partially ameliorated 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, which included independent animals on the UPSA, those with home ranges overlapping the UPSA, and others on adjacent management units. We found that hunters exhibited selection for males, which reduced their 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. Abundance increased with the absence of hunting on the UPSA and protection of marked pumas in adjacent management units. This occurred even with other natural and human causes of mortality acting on the animals. 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., $\lambda = 1.25$ and 1.39, respectively), suggested that if the population continued to be protected from hunting, abundance would likely have increased further. Theoretically, had the non-hunted puma population been naturally limited by food and regulated by competition, growth would have declined (Logan 2019, Ruth et al. 2019). The decline, however, could follow a 4–8-year time lag (Laundré 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. 12). At one end of the spectrum, a study in Utah revealed that abundance of independent pumas in the Monroe Mountains declined by >50% 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 population increased over the next 3 years 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 case, density-dependent population growth (*sensu* Logan and Sweanor 2001) might have regulated the rate of population recovery. In Washington, Beausoleil et al. (2016)
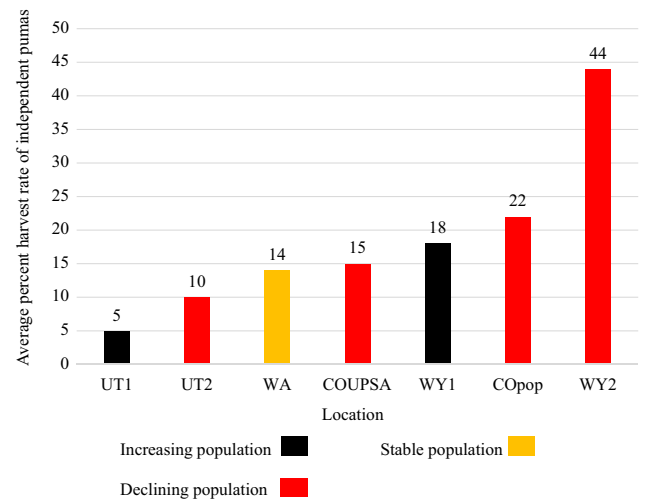
Figure 12. Average percent harvest rates of independent pumas associated with population trends in North America. Location designations refer to 2 harvest periods in 1 population in Utah (UT1 and UT2; Wolfe et al. 2016), a study in Washington (WA; Beausoleil et al. 2016), our Uncompahgre Plateau Study Area (UPSA) average harvest rate (COUPSA), our average population-scale harvest rate (COpop), and 2 harvest periods in 1 population in Wyoming (WY1 and WY2; Anderson and Lindzey 2005).

estimated puma density and found the 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 population sizes and harvest rates should be considered when minimum 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 differences in capacities for population growth (i.e., ecological carrying capacity; *sensu* Fryxell et al. 2014), other competing carnivores, regional population demographics, management actions at local and regional scales, parameter definitions, and population segment scales used in harvest rate estimation. Our study reveals how these latter 3 factors influenced estimated harvest rates.

Consistent with other research, we found that 21% of adult females in the total harvest at the population scale and 23% at the UPSA scale resulted in a 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).

Mortality and Survival

In the absence of hunting on the UPSA, adult pumas died primarily of natural causes, especially intraspecific killing, 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 adults of both sexes 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 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 population sizes 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 greatly increased over that in the reference period, primarily from hunting. Moreover, abundances of adult and independent pumas, and survival of adults and subadult males 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. 2009b) and Montana (Robinson et al. 2014) directly addressed this issue and concluded that hunting mortality was additive at the puma population sizes and harvest rates 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 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 has not been investigated. There may also be an extra-additive mortality effect (Creel and Rotella 2010) operating at increased rates of female harvest. When mothers with litters die, their cubs will also likely be lost (as in our study), which will reduce potential recruitment to the population.

Adult males on the UPSA were the most affected by hunting because of hunter selection. Within 4 years their annual survival and total winter abundance was reduced by more than half, including an almost halving in abundance of adult males <6 years old and likely elimination of males >6 years old. 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 occasions. 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 to likely 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, Newbolt et al. 2017, Bischof et al. 2018, Van de Kerk et al. 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. 13; Table 15). An exception is a puma population in competition with wolves and grizzly bears 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.

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. 2009a, Robinson et al. 2014, respectively). Adult females in our study were not affected as much by hunting as were adult males because of 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 owing to the deaths of mothers.
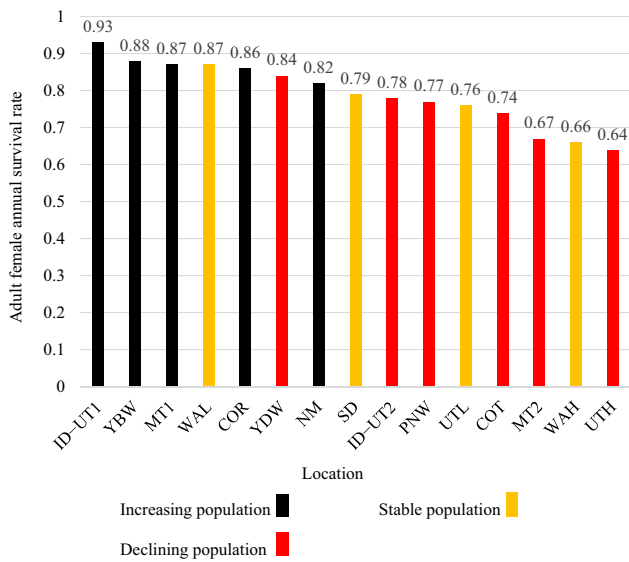
Figure 13. Adult female puma annual survival rates associated with population trends in North America. Location designations refer to Idaho and Utah (ID–UT1 and ID–UT2; Laundré et al. 2007), the Greater Yellowstone Northern Range before and during occupation by wolves (YBW and YDW, respectively; Ruth et al. 2011, 2019), Montana (MT1 and MT2; Robinson and DeSimone 2011), Washington low and high harvest (WAL and WAH, respectively; Cooley et al. 2009b), our reference period and treatment period (COR and COT, respectively), New Mexico (NM; Logan and Sweanor 2001), South Dakota (SD; Jansen 2011), Pacific Northwest (PNW; Lambert et al. 2006), and Utah low and high harvest (UTL and UTH, respectively; Stoner et al. 2006).

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; Table 15). 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. 2009b). 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 because most 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. We observed that infanticide was primarily associated with males and tended to be higher in the reference period with an increasing abundance of adult males and lower 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 because of 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 re-establishment and population recovery, can result in increased [puma cub] mortality." Presumably this would occur as adult

males 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 territorial stability, however, because adult male territoriality was unstable in the reference and treatment periods.

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 reproductive response associated with hunting mortality. Furthermore, there is no evidence that reproduction compensates for hunting mortality in pumas elsewhere in North America (Table 16). Data from our study, 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. (2009b) 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. In South Dakota, males were favored in the non-hunted condition (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, 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 half (Logan and Sweanor 2001). Both in Washington (Cooley et al. 2009b) and Montana (Robinson et al. 2014), mean maternity rates (i.e., kittens/adult female/yr) did not differ between lightly hunted and heavily hunted, or hunted and non-hunted populations, respectively.

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). In contrast, 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, 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 (May–Aug) 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 (Laundré and Hernández 2007) and in Montana (Robinson and

Table 15. Estimated annual and life-stage puma survival rates for males (M) and females (F) in hunted and non-hunted populations in North America, 1992–2020.

Location	Adults non-hunted	Adults hunted	Subadults non-hunted	Subadults hunted	Cubs	Reference
Colorado	0.86 F 0.96 M	0.74 F 0.40 M	0.63 F 0.92 M	0.70 F 0.43 M	0.51[a] 0.14[b]	This study
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 0.63 M	NA	NA	NA	Moss et al. (2016)
California	0.56[d]	NA	0.56[d]	NA	0.56[d]	Vickers et al. (2015)
Florida	0.87 prime F 0.76 old F 0.80 prime M 0.64 old M	NA	0.95 F 0.71 M		0.32	Hostetler et al. (2010) Benson et al. (2011)
New Mexico	0.82 F 0.91 M	NA	0.88 F 0.56 M	NA	0.64	Logan and Sweanor (2001)
Utah	NA	0.64 F and M[e] 0.76 F and M[f]	NA	NA	NA	Stoner et al. (2006)
British Columbia, Idaho and Washington	NA	0.77 F 0.59 M	NA	0.32 F 0.37 M	NA	Lambert et al. (2006)
Idaho and Utah	NA	0.93 F[g] 0.78 F[h]	NA	NA	0.86[g] 0.57[h]	Laundré et al. (2007)
Washington		0.87 F[i] 0.65 M[i] 0.66 F[j] 0.48 M[j]	NA	0.76 F[i] 0.51 M[i] 1.00 F[j] 0.54 M[j]	0.72 F[i] 0.53 M[i] 0.32 F[j] 0.31 M[j]	Cooley et al. (2009b)
Greater Yellowstone Northern Range	NA	0.88 F[k] 0.75 M[k] 0.84 F[l] 0.68 M[l]	NA	NA	0.46[k] 0.59[l]	Ruth et al. (2011)
Montana	NA	0.67 F 0.72 M	NA	0.49 F 0.39 M	0.49 F 0.76 M	Robinson and DeSimone (2011)
South Dakota	0.90 F 0.70 M	0.79 F 0.40 M			0.52[m]	Jansen (2011)
	0.86 F 0.89 M	NA	1.0 F 0.63 M	NA	0.67	Thompson et al. (2014)
Oregon	NA	0.84–0.86 F[n] 0.57 M[o] 0.78–0.86 M[p]	NA		0.66	Clark et al. (2014a, 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] Not applicable.
[d] Survival was constant across age stage, sex, and population segment.
[e] Monroe Mountains, Utah.
[f] Oquirrh Mountains, 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).

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). Female pumas are polyestrous (i.e., cycle into reproductive receptivity continually until pregnant) and some mothers may lose entire litters at any time, which allows for some births to occur outside of the peak periods. Females can resume estrous within as few as 1–3 weeks and usually in 3–4 months after loss of a litter (Logan and Sweanor 2001, Ruth et al. 2019).

Table 16. Puma reproduction parameter estimates in hunted and non-hunted populations, North America, 1983–2020.

Parameter	Average	Hunting status	Range	95% CI	Sample sizes	State or Province	Reference
Gestation (days)	90.4–91.8	Combined[a]	84–95	89.1–92.9	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 (months)	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 first conception (months)	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 first litter (months)	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)
	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. (2009b)
	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)
Male:female 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. (2009b)
	0.51	Light hunting	NA	NA	6 yrs		
	0.58	Combined	NA	NA	9 yrs	MT	Robinson and DeSimone (2011)

[a] Data were compiled over hunted and non-hunted time periods.
[b] Not applicable.
[c] A minimum quantity was reported.
[d] Pumas were removed alive and translocated, resulting in a 50% reduction in the adult puma population.

Recruitment

Puma population growth on the UPSA was affected by recruitment of young females and males 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. 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 subadults emigrating from the UPSA and expected other subadults were

moving into the UPSA. Recruitment in the reference period resulted in an increasing abundance of adults. 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 adults, 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 displayed 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 females, that females and males 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 (Newby et al. 2013, Stoner et al. 2013). Philopatric males apparently occur more frequently in Southern California and Florida where puma habitat is fragmented by human development to the extent of obstructing or constricting dispersal movements (Beier et al. 1995, Maehr 1997, respectively). Dispersal by pumas, especially of males, is important in inbreeding avoidance and gene flow (Biek et al. 2006). Consequences of disrupted dispersal, as in pumas in California, include lower genetic diversity and strong population genetic structuring (Gustafson et al. 2019). Philopatry in males 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 result in a higher frequency of 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 United States, including New Mexico, Utah, Washington, the Greater Yellowstone Northern Range, the Great Basin, and Montana (Sweanor et al. 2000, Stoner et al. 2006, Cooley et al. 2009a, 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. 2009a, 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 because of the connectedness of 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.

Associated with these dynamics, a source-sink model is recognized as biologically valid for depicting spatial variation of risk and inter-population connectivity for large carnivores including the puma (Sweanor et al. 2000, Laundré and Clark 2003, Cooley et al. 2009a, Ruth et al. 2011, Newby et al. 2013), black and grizzly bears (Draheim et al. 2016, Schwartz et al. 2010, respectively), wolf (Schmidt et al. 2017), and African lion (Panthera leo; Sinclair 1995). In a source-sink structure hunting mortality occurs 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). Lower survival of pumas (Ruth et al. 2011), grizzly bears (Schwartz et al. 2010), African lions (Loveridge et al. 2010), and wolves (Schmidt et al. 2017) has been associated with movements of these animals from source areas to adjacent sink areas with higher human-caused mortality.

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 population with very few animals >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 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 or experimental removal 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. 2009b), 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 therefore generally outnumber adult males, which have large territories (Seidensticker et al. 1973, Logan and Sweanor 2001). Cubs are the second most abundant segment in winter, although they may be more abundant in the summer. This is because a large majority of mortalities occur when cubs are ≤5 months old and prior to their first winter (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 puma population structure in winter in New Mexico (Logan and Sweanor 2001), Utah and Idaho (Laundré 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, Laundré and Hernández 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, 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 subadults emigrated primarily during March to June in association with heightened breeding behavior of adults.

Puma Hunters

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 animal prior to deciding whether or not to kill it. Hunters were likely able to distinguish sex because of experience and sex identification material provided to them through the CPW puma education and identification course made mandatory since 2007 (CPW 2017). Similarly, experienced 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 males even though they generally encountered fresh tracks of females more frequently than those of males, and females were more abundant. Our researchers' observations of more fresh tracks of females than of 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 males as a group are more vulnerable to hunting with dogs because hunters detect tracks of males more frequently than those of females (*sensu* Anderson and Lindzey 2005). Instead, it is more likely that males are more vulnerable because of selection by hunters using dogs. Hunters in Washington killed more males than females 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. (2014a:785) found that hunting 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."

Hunter participation on the UPSA was highest when the harvest quota and puma abundance were high and lowest when the quota and abundance were low. Hunters used similar efforts to kill males and females 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 abundance were lowest likely because of a reduced chance of encountering independent pumas, especially preferred adult males.

Hunter selection resulted in demographic effects that included substantially 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).

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 abundance. Puma abundance is the basic parameter that managers must consider either empirically, or theoretically in harvest management. Prevalent in their range, however, are non-surveyed regions where managers routinely extrapolate population parameter estimates derived from the literature. Density assumptions are commonly extrapolated, 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 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, Murphy et al. 2019).

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 detected and some human-caused deaths (e.g., vehicle strikes, illegal killing) go unobserved. In addition, hunting deaths may not be compensated by increased survival, reproduction, and immigration (this study, Cooley et al. 2009a, Robinson et al. 2014, Wolfe et al. 2015). In areas managed 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.

Regulated hunting used to manipulate abundance in smaller management units to address local issues (e.g., over-kill of adult females, 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, abundance declined when all independent pumas were legal game in the UPSA and surrounding

management units. Moreover, emigrating 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 immigrants from just as far away. However, the emigration, dispersal distance, and establishment success of pumas could be negatively affected by human-caused mortality, particularly from heavy harvest (Newby et al. 2013). Therefore, larger regions for management purposes are more appropriate to the scale of puma movements and demographics. In our study system, that region ranged from about 11,600 km^2 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 population state).

Results from our study revealed how the management outcome at the population scale can diverge from the stated objective and assumptions. To address this, managers could apply adaptive management (Walters 1986, Williams et al. 2001) to hunting and further learn its effects on puma behavior and populations. Besides informing puma management (e.g., Montana Fish, Wildlife, and Parks 2019), this process is also recommended for other harvested felids including African leopard (*P. pardus*; Balme et al. 2010) and Eurasian lynx (*Lynx lynx*; Linnell et al. 2010). In so doing, managers examine relationships of response variables (e.g., puma survival rates, ungulate survival rates, puma predation rates) to estimates of puma abundance or harvest data (e.g., Anderson and Lindzey 2005, Hurley et al. 2011, Wolfe et al. 2016), thus enabling them to apply the best available information and practices to puma management (Cougar Management Guidelines Working Group 2005, Jenks 2011).

Puma population dynamics in our study fit a source-sink management model, which can provide for conservation, hunting opportunity, options for mitigating conflicts with humans and other wildlife, and a framework for research (Logan and Sweanor 2001, Wyoming Game and Fish 2006, Robinson et al. 2008, Cooley et al. 2011, Robinson et al. 2014, Ruth et al. 2019). Similarly, a source-sink approach was developed for managing leopards in South Africa (Balme et al. 2010). Because managers rely upon assumptions about puma populations and effects of hunting in areas unless they are surveyed, they should consider the extents of areas managed with objectives for population reduction relative to those managed for stable or increasing abundance when puma conservation is a state-wide goal (Novaro et al. 2005). There are some likely protected (e.g., national parks and monuments, state parks) and lightly hunted areas already on the landscape. Managers need to reckon the validity of those as sources, however, 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).

Selective hunters using dogs and trained in sex identification of pumas could influence population demographics and facilitate 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 survival, reduce adult male abundance, and create a younger age structure. As puma abundance and the male component declines further, however, hunter selection and encounters with males are expected to diminish and 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 life-history strategies are deemed important for adaptive potential, conservative harvest rates and pursuit-only opportunities could be applied in an effort to maintain a natural population structure. Dispersal of non-selected pumas from those 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.

ACKNOWLEDGMENTS

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, Fort 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, Fort 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 M. Hornocker and S. Negri, editors. Cougar: ecology & conservation. 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. Washington Department of Fish and Wildlife, Olympia, 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.

Balme, G. A., L. T. B. Hunter, P. Goodman, H. Ferguson, J. Craigie, and R. Slotow. 2010. An adaptive management approach to trophy hunting of leopards (Panthera pardus): a case study from KwaZulu-Natal, South Africa. Pages 341–352 in D. W. Macdonald and A. J. Loveridge, editors. Biology and conservation of large felids. Oxford University Press, Oxford, United Kingdom.

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 189:577–586.

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., 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.

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.

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. Wyoming Game and Fish Department, Lander, USA.

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

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

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. University of Arizona Press, Tucson, USA.

Brown, E. E., and C. A. López González. 2001. Borderland jaguars. University of Utah Press, Salt Lake City, 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, 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, and D. H. Jackson. 2015. Monthly and annual survival rates of cougar kittens in Oregon. Northwest Science 89:393–400.

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

Clark, S. G., M. B. Rutherford, and D. J. Mattson. 2014b. Large carnivores, people, and governance. Pages 1–28 in S. G. Clark and M. B. Rutherford, editors. Large carnivore conservation: integrating science and policy in the North American West. Chicago Press, Chicago, Illinois, USA.

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

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

Colorado Parks and Wildlife [CPW]. 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., 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.

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

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

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

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.

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.

Dorfman, R. 1938. A note on the δ-method for finding variance formulae. The Biometric Bulletin 1:129–137.

Draheim, H. M., J. A. Moore, D. Etter, S. R. Winterstein, and K. T. Scribner. 2016. Detecting black bear source-sink dynamics using individual-based genetic graphs. Proceedings of the Royal Society B 283:20161002.

Efford, M. 2004. Density estimation in live-trapping studies. Oikos 106:598–610.

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.

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.

Elbroch, L. M., and H. U. Wittmer. 2012. Table scraps: inter-trophic food provisioning by pumas. Biology Letters 8:776–779.

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, Chicago, 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, et al. 2019. Genetic 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.

Ivan, J. S., G. C. White, and T. M. Shenk. 2013. Using auxiliary telemetry information to estimate animal density from capture–recapture data. Ecology 94:809–816.

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

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

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225–248.

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, D. 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.

Kendall, W. L. 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. Ecology 80:2517–2525.

Kreeger, T. J., J. M. Arnemo, and J. P. Raath. 1999. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals, Fort Collins, Colorado, 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. 2010. Behavioral response races, predator–prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. Ecology 9:2995–3007.

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., and L. Hernández. 2003. Factors affecting dispersal in young male pumas. Pages 151–160 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.

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., 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., L. Hernández, D. Streubel, K. Altendorf, and C. L. Lopez Gonzalez. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.

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, 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.

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.

Linnell, J. D. C., H. Broseth, J. Odden, and E. B. Nilsen. 2010. Sustainably harvesting a large carnivore? Development of Eurasian lynx populations in Norway during 160 years of shifting policy. Environmental Management 45:1142–1154.

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

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, Chicago, Illinois, USA.

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. Colorado Parks and Wildlife, Estes Park, USA.

Loveridge, A. J., G. Hemson, Z. Davidson, and D. W. Macdonald. 2010. African lions on the edge: reserve boundaries as "attractive sinks". Pages 283–304 in D. W. Macdonald and A. J. Loveridge, editors. Biology and conservation of wild felids. Oxford University Press, Oxford, United Kingdom.

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 S. A. Becker, D. D. Bjornlie, F. G. Lindzey, and D. S. Moody, editors. Proceedings of the Seventh Mountain Lion Workshop. Wyoming Game and Fish Department, Lander, USA.

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

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

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.

Murphy, S. M., D. T. Wilkins, B. C. Augustine, M. A. Peyton, and G. C. Harper. 2019. Improving estimation of puma (*Puma concolor*) population density: clustered camera-trapping, telemetry data, and generalized spatial mark-resight models. Scientific Reports 9:4590.

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. 2008. Idaho mountain lion status report. Pages 8–17 in D. Toweill, S. Nadeau, and D. Smith, editors. Proceedings of the 9th Mountain Lion Workshop. Idaho Department of Fish and Game, Sun Valley, USA.

Negri, S., and H. Quigley. 2010. Cougar conservation: the growing role of citizens and government. Pages 221–234 in M. Hornocker and S. Negri, editors. Cougar: ecology & conservation. 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, et al. 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 S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, 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., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107.

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.

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.

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.

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.

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., P. C. Buotte, and M. G. Hornocker. 2019. Yellowstone cougars: ecology before and during wolf restoration. University Press of Colorado, Boulder, 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., and K. Murphy. 2010. Cougar-prey relationships. Pages 138–162 in M. Hornocker and S. Negri, editors. Cougar: ecology & conservation. Chicago Press, Chicago, Illinois, USA.

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

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

Schmidt, J. H., J. W. Burch, and M. C. MacCluskie. 2017. Effects of control on the dynamics of an adjacent protected wolf population in Interior Alaska. Wildlife Monographs 198:1–30.

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 D. R. McCullough, K. Kaji, and M. Yamanaka, editors. Wildlife in Shiretoko and Yellowstone National Parks: lessons in wildlife conservation from two World Heritage Sites. Shiretoko Nature Foundation, Hokkaido, Japan.

Schwartz, C. C., M. A. Haroldson, and G. C. White. 2010. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. Journal of Wildlife Management 74:654–667.

Schwarz, C. J., and W. T. Stobo. 1997. Estimating temporary migration using the robust design. Biometrics 53:178–194.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52:249–260.

Sikes, R. S., and 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.

Sinclair, A. R. E. 1995. Serengeti past and present. Pages 3–33 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management and conservation of an ecosystem. Chicago University Press, Chicago, Illinois, USA.

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

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, 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.

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

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. Washington Department of Fish and Wildlife, Olympia, 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:e0131490.

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

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

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. Washington Department of Fish and Wildlife, Olympia, 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., 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.

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.

Woodroffe, 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, New York, New York, USA.

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

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.