




Integrated Carnivore-Ungulate Management: A Case Study in West-Central Montana

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ABSTRACT Understanding the effectiveness of harvest regulations to manipulate population abundances is a priority for wildlife managers, and reliable methods are needed to monitor populations. This is particularly true in controversial situations such as integrated carnivore-ungulate management. We used an observational before-after-control-treatment approach to evaluate a case study in west-central Montana, USA, that applied conservative ungulate harvest together with liberalized carnivore harvest to achieve short-term decreases in carnivore abundance and increases in ungulate recruitment. Our study areas included the Bitterroot treatment area and the Clark Fork control area, where mountain lion populations (*Felis concolor*) were managed for a 30% reduction and for stability, respectively. The goals of the mountain lion harvest were to provide a short-term reduction of mountain lion predation on elk (*Cervus canadensis*) calves and an increase in elk recruitment, elk population growth rate, and ultimately elk abundance. We estimated mountain lion population abundance in the Bitterroot treatment and Clark Fork control areas before and 4 years after implementation of the 2012 harvest treatment. We developed a multi-strata spatial capture-recapture model that integrated recapture and telemetry data to evaluate mountain lion population responses to harvest changes. Mountain lion abundance declined with increasing harvest in the Bitterroot treatment area from 161 (90% credible interval [CrI] = 104, 233) to 115 (CrI = 69, 173). The proportion of males changed from 0.50 (CrI = 0.33, 0.67) to 0.28 (CrI = 0.17, 0.40), which translated into a decline in the abundance of males, and similar abundances of females (before: males = 80 [CrI = 52, 116], females = 81 [CrI = 52, 117]; after: males = 33 [CrI = 20, 49], females = 82 [CrI = 49, 124]). In the Clark Fork control area, an area twice as large as the Bitterroot treatment area, we found no evidence of changes in overall abundance or proportion of males in the population. The proportion of males changed from 0.42 (CrI = 0.26, 0.58) to 0.39 (CrI = 0.25, 0.54), which translated into similar abundances of males and females (before: males = 24 [CrI = 16, 36], females = 33 [CrI = 21, 39]; after: males = 28 [CrI = 18, 41], females = 44 [CrI = 29, 64]). To evaluate if elk recruitment and population growth rate increased following treatment, we developed an integrated elk population model. We compared recruitment and population growth rate during the 5 years prior to and 5 years following implementation of the mountain lion harvest treatment for 2 elk populations within the Bitterroot treatment area and 2 elk populations within the Clark Fork control area. We found strong evidence that temporal trends differed between the 2 areas. In the Bitterroot treatment area, *per capita* elk recruitment was stable around an estimated median value of 0.23 (CrI = 0.17, 0.36) in the pre-treatment period (2007–2011), increased immediately after treatment (2013) to 0.42 (CrI = 0.29, 0.56), and then declined to 0.21 (CrI = 0.11, 0.32) in 2017. In contrast, *per capita* elk recruitment estimates in the Clark Fork control area had similar median values during the pre- (2007–2011: 0.30, CrI = 0.2, 0.35) and post-treatment periods (2013–2017: 0.31, CrI = 0.26, 0.36). These changes in recruitment corresponded to similar changes in elk population growth rate, although population growth rates were also subject to variation due to changing elk harvest. In the Bitterroot treatment area, population growth rates in the pre-treatment period were stable to slightly declining, with an estimated median value of 0.92 (CrI = 0.88, 1.07) in the pre-treatment period (2007–2011). Population growth rate during the post-treatment period increased immediately after treatment (2012: 1.17, CrI = 1.14, 1.20) prior to declining to 1.06 (CrI = 1.04, 1.09) in 2016. In contrast, the median population growth rates were roughly equal in the Clark Fork control area during the pre-treatment period (1.01, CrI = 0.86, 1.09) from 2007 to 2011 and post-treatment period (1.00, CrI = 0.83, 1.15) from 2013 to 2017. Together, these results indicate that the harvest treatment achieved a moderate (i.e., 29%) reduction in mountain lion population abundance within the treatment area that

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corresponded with short-term increases in elk recruitment and population growth. Elk population demographic responses suggest that the harvest treatment effect was strongest immediately after the mountain lion harvest treatment was implemented and lessened over time as the harvest treatment was reduced. This suggests that the short-term harvest treatment resulted in short-term demographic responses in elk populations, and more sustained harvest treatments would be necessary to achieve longer-term elk population demographic responses. We recommend that wildlife managers seeking to balance carnivore and ungulate population objectives design rigorous carnivore and ungulate population monitoring programs to assess the effects of harvest management programs. Assessing and understanding effects of carnivore harvest management programs will help to set realistic expectations regarding the effects of management programs on carnivore and ungulate populations and allow managers to better design programs to meet desired carnivore and ungulate population objectives.

KEY WORDS carnivore management, *Cervus canadensis*, elk, elk survival, hunting, population model, *Puma concolor*, spatial capture-recapture.

Gestion Intégrée des Carnivores et des Cervidés: Une Étude de Cas dans le Centre-Ouest du Montana

RÉSUMÉ Comprendre l'efficacité des règlements de récolte à contrôler l'abondance des populations est une priorité pour les gestionnaires de la faune, et des méthodes fiables sont nécessaires pour suivre l'état des populations. Cela est particulièrement vrai face à des situations controversées telles que la gestion intégrée des carnivores et des cervidés. Nous avons utilisé une approche observationnelle avant-après-témoin-traitement dans le cadre d'une étude de cas prenant place dans le centre-ouest du Montana, aux États-Unis. L'étude impliquait une récolte de cervidés conservatrice et une récolte de carnivores plus permissive afin de réduire l'abondance des carnivores à court terme et d'augmenter le recrutement de cervidés. Nos aires d'étude comprenaient la zone expérimentale de la Bitterroot où la gestion visait à réduire les populations de cougars (*Felis concolor*) de 30%, ainsi que la zone témoin de Clark Fork où l'objectif était de maintenir des populations stables. La récolte de cougars visait la réduction à court terme de la prédation sur les faons de wapitis (*Cervus canadensis*), tout en augmentant le recrutement de wapitis, de même que le taux de croissance et l'abondance de leur population. Nous avons estimé l'abondance des cougars dans la zone de traitement de la Bitterroot et dans la zone témoin de Clark Fork avant la mise en œuvre du traitement de récolte en 2012, puis 4 ans après. Nous avons développé un modèle spatial de capture-marquage-recapture pour population stratifiée qui intégrait des données de recapture et de télémétrie afin d'évaluer comment la population de cougars réagit aux variations du taux de récolte. L'abondance de cougars a diminué avec l'augmentation de la récolte dans la zone de traitement de la Bitterroot, passant de 161 (intervalle de crédibilité à 90% [ICr] = 104, 233) à 115 (ICr = 69, 173). La proportion de mâles est alors passée de 0,50 (ICr = 0,33, 0,67) à 0,28 (ICr = 0,17, 0,40), ce qui reflète la diminution de l'abondance des mâles et le maintien de l'abondance des femelles (avant: mâles = 80 [ICr = 52, 116], femelles = 81 [ICr = 52, 117]; après: mâles = 33 [ICr = 20, 49], femelles = 82 [ICr = 49, 124]). Dans la zone témoin de Clark Fork, une zone deux fois plus grande que la zone de traitement de la Bitterroot, nous n'avons détecté aucun changement dans l'abondance des mâles ou dans leur proportion au sein de la population. La proportion de mâles est passée de 0,42 (ICr = 0,26, 0,58) à 0,39 (ICr = 0,25, 0,54), se traduisant par une abondance similaire entre les mâles et les femelles (avant: mâles = 24 [ICr = 16, 36], femelles = 33 [ICr = 21, 39]; après: mâles = 28 [ICr = 18, 41], femelles = 44 [ICr = 29, 64]). Pour évaluer si le recrutement de wapitis et le taux de croissance de leur population ont augmenté suite au traitement, nous avons développé un modèle intégré des populations de wapitis. Nous avons comparé le taux de recrutement et de croissance de 4 populations de wapitis au cours des 5 années qui ont précédé et des 5 qui ont suivi le début de la récolte de cougars. Deux populations de wapitis se situaient dans la zone de traitement de la Bitterroot et 2 dans la zone témoin de Clark Fork. Nos résultats suggèrent fortement que les variations temporelles des populations différaient entre les 2 aires d'étude. Dans la zone de traitement de la Bitterroot, le recrutement des wapitis par individu était stable autour d'une valeur médiane de 0,23 (ICr = 0,17, 0,36) durant la période de prétraitement (2007–2011), il a augmenté suite au traitement pour atteindre un niveau intermédiaire de 0,42 (ICr = 0,29, 0,56) en 2013, puis il a diminué à 0,21 (ICr = 0,11, 0,32) en 2017. En revanche, le recrutement des wapitis par individu avait des valeurs médianes similaires durant les périodes pré- (2007–2011: 0,30, ICr = 0,2, 0,35) et de post-traitement (2013–2017: 0,31, ICr = 0,26, 0,36) dans la zone témoin de Clark Fork. Les variations du recrutement étaient liées à des changements similaires dans le taux de croissance des populations de wapitis, bien que le taux de croissance des populations ait également varié suite aux variations de récolte de wapitis. Dans la zone de traitement de la Bitterroot, les taux de croissance des populations étaient stables ou légèrement en baisse durant la période de prétraitement (2007–2011), avec une valeur médiane de 0,92 (ICr = 0,88, 1,07). Le taux de croissance de la population a augmenté immédiatement après le traitement (2012: 1,17, ICr = 1,14, 1,20), avant de diminuer à 1,06 (ICr = 1,04, 1,09) en 2016. En revanche, le taux de

croissance médian des populations de la zone témoin de Clark Fork est demeuré semblable entre la période prétraitement (1,01, ICr = 0,86, 1,09) de 2007 à 2011 et celle post-traitement (1,00, ICr = 0,83, 1,15) de 2013 à 2017. Globalement ces résultats indiquent que le traitement de récolte a permis une réduction modérée (c.-à-d. 29%) de l'abondance des couguars dans la zone expérimentale, de même qu'une augmentation à court terme à la fois du recrutement et de la taille de la population de wapitis. Les changements démographiques de la population de wapitis suggèrent que l'effet du traitement de récolte a été maximal immédiatement après le début du traitement de récolte de couguars, puis a graduellement diminué suivant la réduction du taux de récolte. Ce résultat suggère que le traitement de récolte a eu une influence à court terme sur la démographie des populations de wapitis et, par conséquent, qu'un traitement de récolte plus soutenu serait nécessaire pour espérer un impact à plus long terme. Nous recommandons aux gestionnaires de la faune qui visent à gérer à la fois les populations de carnivores et de cervidés, de concevoir des programmes de surveillance permettant une évaluation rigoureuse des effets de la récolte sur ces populations. L'évaluation et la compréhension de l'effet des programmes de gestion de la récolte des carnivores aideront à établir des attentes réalistes quant aux effets de ces programmes sur les populations de carnivores et de cervidés, tout en permettant aux gestionnaires de concevoir des programmes permettant de mieux rencontrer les objectifs de gestion pour toutes ces populations.

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INTRODUCTION

The recovery of many carnivore species worldwide represents a conservation success made possible through protective legislation, adequate funding, supportive public opinion, and management practices that allow large carnivores and people to coexist (Weber and Rabinowitz 1996, Swenson et al. 1998, Franklin et al. 1999, Walker et al. 2010, Chapron et al. 2014). However, the conservation and management of carnivores is challenging as they may require large amounts of habitat, create human-wildlife conflicts, and have important effects on prey communities (Noss et al. 1996, Treves and Karanth 2003, Lucherini and Merino 2008, Kaartinen et al. 2009). The recovery of large carnivores such as wolves (*Canis lupus*), mountain lions (*Felis concolor*), and grizzly bears (*Ursus arctos*) in North America is important in part because predation has been shown to be a proximate limiting and regulating factor for many ungulate populations (Messier 1994, Hebblewhite et al. 2002, Garrott et al. 2008, Andren and Liberg 2015). Ungulates are iconic species throughout the world and play a large role across ecological (Augustine and McNaughton 1998, Frank and Groffman 1998, Du Toit and Cumming 1999, Kauffman et al. 2010), social (Haggerty and Travis 2006), and economic

(Duffield and Holliman 1988, Gordon et al. 2004, U.S. Department of the Interior 2011) landscapes. The recovery of large carnivores and concerns regarding potential effects of predation on ungulate populations have presented challenges for wildlife management.

Since the early 2000s, declines in ungulate populations in some parts of the western United States have resulted in growing concerns that the concurrent recovery of large carnivores has depressed ungulate populations (White and Garrott 2005, Barber-Meyer et al. 2008, White et al. 2010, Griffin et al. 2011). To develop effective management actions to reverse population declines, wildlife managers need to identify the vital rates having the greatest influence on population growth, and the factors affecting those vital rates. The influence of a vital rate on population growth rate (λ) is determined by the effect of proportional changes in the vital rate on λ (i.e., elasticity; de Kroon et al. 1986) and the variability of the vital rate (Gaillard et al. 2000). Vital rates with higher variability can have a relatively larger influence on population growth because they can translate to higher variation in population growth and dampen growth over time (Mills et al. 1999, Coulson et al. 2005). Ungulate population growth rate is most sensitive to changes in

adult female survival (Eacker et al. 2017); however, in unharvested populations adult female survival is generally high and varies little over time (Gaillard et al. 2000, Brodie et al. 2013). In contrast, juvenile recruitment often shows higher variability and explains more of the variation in population growth rates (Gaillard et al. 2000, Raithel et al. 2007). For ungulate populations, much of the variation in population growth rates is explained by variation in juvenile survival (Gaillard et al. 1998, 2000; Raithel et al. 2007). Yet, where adult survival does vary in response to harvest, predation, or climate, it can be a significant driver (Owen-Smith and Mason 2005, Nilsen et al. 2009, Eacker et al. 2017). Regardless of which vital rate is the dominant driver of population growth rates in ungulates, juvenile survival plays a key role in population dynamics and factors, such as predation and weather, that influence juvenile survival may have important effects on population trajectories.

To achieve population abundance goals and address concerns regarding effects of predation, wildlife managers may design integrated carnivore-ungulate harvest management programs. Integrated carnivore-ungulate management programs use a combination of liberalized carnivore and restrictive ungulate harvest regulations to achieve population abundance goals. These differ from predator control programs in that liberalized carnivore and restrictive ungulate harvest regulations are prescribed and achieved through hunting, whereas predator control programs typically apply liberalized carnivore harvest regulations without adjusting ungulate harvest regulations, and may use a combination of hunters or management staff to achieve reductions. Assumptions underlying the prescription of an integrated carnivore-ungulate harvest management program include 1) increased harvest reduces the abundance of the carnivore population, 2) the carnivore population reduction results in a reduction of the carnivore-specific ungulate predation rate (defined as the product of the killing rate and carnivore numeric response that translates as mortality rate; Messier 1994), 3) reductions in the harvest of ungulates contribute to increased vital rates, and 4) the reduction in total predation rate (from both human hunting and large carnivores) results in increases in key vital rates that increase the ungulate population growth rate. If all assumptions are valid, then integrated carnivore-ungulate harvest management programs can be a useful tool for wildlife managers seeking to increase ungulate abundance.

Carnivore management programs designed to reduce carnivore populations and increase ungulate recruitment and population growth have been implemented in a variety of ecological systems from the boreal forest to sagebrush-steppe ecosystems (Schwartz et al. 2003, Hurley et al. 2011). However, effects of these management programs on ungulate populations are debated and effects vary across ecological systems (Boertje et al. 1996, Hayes et al. 2003, White et al. 2010, Hurley et al. 2011, Keech et al. 2011, Tatman et al. 2018). Multiple, multi-year studies of bear-wolf-moose (*Alces alces*) systems in Alaska, USA, found that predation was the dominant factor affecting moose survival and abundance, and, in many cases, experimental reductions of predators increased populations (see Boertje et al. 2010 for review; but see also Hayes et al. 2003). In the Rocky Mountains, an experimental study in a bear-mountain lion-elk (*Cervus canadensis*) system found increased bear and mountain lion

harvest increased elk calf survival (White et al. 2010), though effects of predator harvest on their populations were not directly assessed. Yet, also in the Rocky Mountains, an experimental study in a coyote-mountain lion- mule deer (*Odocoileus hemionus*) system found only short-term, weak responses of survival and abundance following coyote (*Canis latrans*) and mountain lion reductions (Hurley et al. 2011). Although public attention is often focused on the effects of wolf recovery on ungulate populations, the effects of recovering wolf populations on ungulate populations vary from relatively minor effects reported in some studies (Vucetich et al. 2005, Barber-Meyer et al. 2008, White et al. 2010, Eacker et al. 2016) to more important effects reported in others (Hebblewhite et al. 2002, Garrott et al. 2008, Horne et al. 2019). These results highlight the need for wildlife managers to better understand the uncertainties associated with carnivore effects on ungulate populations, which ultimately influence the efficacy of integrated carnivore-ungulate management programs. Multiple factors affect the efficacy of integrated carnivore-ungulate management, including the magnitude of the harvest treatments, duration of the carnivore control treatment, weather conditions during and after the treatment (Boertje et al. 1996), and interactions with other predators and prey in the system (Arthur and Prugh 2010, Prugh and Arthur 2015).

The utility of harvest management regulations as a tool for reducing carnivore population densities and increasing ungulate recruitment is unknown. Multiple sources of uncertainty exist in the ecological processes and effects of management actions that occur between prescribing carnivore harvest regulations and achieving increases in ungulate recruitment. First, the carnivore harvest objective may not be achievable using hunter harvest (White et al. 2010, Bischof et al. 2012, Tatman et al. 2018). Second, the achieved harvest may not result in a biologically significant change in carnivore abundance (Adams et al. 2008, Robinson et al. 2014). Moreover, in many previous studies of the effects of carnivore management on ungulate populations, changes in both populations harvest and abundance were often not measured, resulting in relatively weak inferences (National Research Council 1997). Third, even if desired carnivore harvest and population levels are achieved, a change in predation rate may not affect ungulate population growth (Garrott et al. 2005, Melis et al. 2009, Boertje et al. 2010). This is related to the degree to which predation mortality is compensatory or additive, and potential effects of other factors such as carrying capacity on survival and recruitment (Singer et al. 1997, Griffin et al. 2011, Brodie et al. 2013). Thus, the efficacy of integrated carnivore-ungulate management varies, making it difficult for wildlife managers to develop and evaluate programs to balance carnivore and ungulate populations at desired levels.

Understanding the biological effects of integrated carnivore-ungulate management requires estimating important parameters of both populations before and after harvest prescriptions are implemented. Evaluating if harvest prescriptions achieve desired carnivore population management goals is a first step in evaluating the efficacy of integrated carnivore-ungulate management. Estimating carnivore population size is challenging because they often occur at low densities, are wide ranging and difficult to detect, and violate the population closure assumption, which is important to traditional capture-recapture

population estimation. Spatial-capture recapture modeling provides an efficient method of estimating carnivore population size (Proffitt et al. 2015, Boulanger et al. 2018, Paterson et al. 2019a) that incorporates the spatial organization of individuals through estimation of trap-specific capture probabilities while also accounting for detection probability (Efford and Fewster 2013, Royle et al. 2013, Efford 2014). These methodologies allow wildlife managers to monitor carnivore population abundances before and after implementing harvest prescriptions and to evaluate if harvest prescriptions meet the management objectives.

Ungulate demography also needs to be evaluated to determine if changes in carnivore abundance result in changes in ungulate vital rates, and, ultimately, growth rate. If ungulate populations are limited by factors such as weather or habitat (Garrott et al. 2003, Griffin et al. 2011, Johnson et al. 2019), or if predation is compensatory with other factors (Singer et al. 2003, Garrott et al. 2008), changes in carnivore populations may not result in changes in the key vital rates, such as recruitment, that drive ungulate population growth rate. The efficacy of integrated carnivore-ungulate programs may be evaluated by monitoring these key ungulate vital rates and population growth pre- and post-harvest treatment. Evaluating the success of a management program in meeting the ungulate population objectives is often achieved through estimation of annual calf survival (e.g., calf: adult female ratios as an index of juvenile recruitment) or population growth rate (e.g., Lukacs et al. 2018). Ungulate population monitoring programs are routinely employed by state wildlife management agencies annually or biannually. However, uncertainty in the relationship between uncorrected count data and true population size (e.g., sightability; Steinhorst and Samuel 1989), and between age ratio data and annual calf survival (Harris et al. 2008), makes the detection of changes in population size and juvenile recruitment challenging. Recent methodical advances allow for count and age ratio data to be used in integrated population models that partition the variance in observations into variation associated with biological and sampling processes to more precisely estimate demographic parameters (Link et al. 2003, Kéry and Schaub 2011, Nilsen and Strand 2018). However, even with new methods available that improve managers' ability to monitor and estimate populations, the uncertainties in the relationship between prescribed carnivore harvest and ungulate population responses make the effectiveness of integrated carnivore-ungulate management programs unknown.

In the western United States, carnivore recovery has resulted in varying effects on elk populations with different carnivore-ungulate assemblages (Garrott et al. 2005). In some areas, bear predation is an important mortality source for elk calves (Raithel 2005, Smith et al. 2006, White et al. 2010, Lukacs et al. 2018), and bear predation on calves has increased over recent decades as bear populations increased (Singer et al. 1997, Barber-Meyer et al. 2008). In other systems, wolf predation (Garrott et al. 2008) or mountain lion predation is the primary mortality source for calves (Myers et al. 1998, Johnson et al. 2013, Eacker et al. 2016, Horne et al. 2019).

In areas dominated by public land in west-central Montana, USA, low recruitment and declining elk abundance raised public

concerns about the effects of increasing carnivore populations on ungulates (Eacker et al. 2016). In response to such low recruitment and declining elk trends in the region, wildlife managers implemented integrated carnivore-ungulate management to reduce carnivore abundances and increase elk recruitment and populations. The management included more restrictive elk harvest intended to reduce the effects of hunter harvest on elk (*sensu* Todd 2002), and more liberal harvest designed to reduce carnivore populations through increases in hunter harvest. In this area, similar to other parts of the western United States, calf recruitment is an important factor affecting elk population growth (Raithel et al. 2007, Eacker et al. 2017), and mountain lion predation is the primary source of calf mortality (Eacker et al. 2016, Forzley 2019).

An objective of the carnivore harvest management program was to reduce mountain lion populations by approximately 30% over the Bitterroot, Blackfoot, and lower Clark Fork watersheds. Mountain lion populations are resilient to harvest and capable of recovering quickly following harvest (Ross and Jalkotzy 1992, Anderson and Lindzey 2005, Robinson et al. 2014, Williams 2018). However, the objective for a 30% reduction represented a short-term strategy for temporarily decreasing mountain lions to boost ungulate populations. Given social controversy surrounding mountain lion harvest objectives, a targeted reduction of >30% was unlikely to be acceptable (Mitchell et al. 2018). In west-central Montana, the estimated female mountain lion harvest rate averaged 7% prior to treatment during 2004–2010, whereas a female mortality rate of approximately 20% or greater is required to produce population declines (Robinson et al. 2014). Therefore, to temporarily reduce populations by 30%, the original management objective was to achieve a 35% harvest rate on adult female mountain lions for 3 years and maintain male harvest opportunity and rates at levels similar to the historical average. Harvest quotas to achieve the targeted 35% rate were designed based on available mountain lion population abundance estimates (Robinson et al. 2015) and social tolerance (Mitchell et al. 2018) and were achieved via liberalized quotas and public hunting seasons. Following the treatment, the management objective was to reduce female harvest rates and manage for stable populations. Because of limited social tolerance for female harvest, the achieved treatment included only 2 years of higher female quotas, followed by reduced female quotas and increased male quotas. The harvest management objectives also included maintaining stable mountain lion populations in the adjacent upper Clark Fork watershed, which was not experiencing declining elk recruitment and growth rate. Additionally, black bear (*Ursus americanus*) harvest was liberalized through a 2-week extension of the spring hunting season that resulted in little change in annual bear harvest and presumably population abundances (Table S1, available online in Supporting Information). Wolf harvest was liberalized immediately following the delisting of wolves in 2011. In spite of liberalized regulations, the wolf population increased and then stabilized with no observed reductions in wolf abundance during the carnivore treatment period (Table S1). There were low rates of black bear and wolf predation on elk calves in the Bitterroot study area (Eacker et al. 2016, Forzley 2019).

To assess the efficacy of integrated carnivore-ungulate management in west-central Montana at increasing elk calf recruitment and population growth rates, our objectives were to 1) evaluate the effects of the mountain lion harvest prescription on mountain lion population abundance, and 2) compare rates of elk calf recruitment and population growth before and after implementation of the mountain lion harvest treatment. To address our first objective, we used a before-after-control-treatment design to evaluate if harvest regulations resulted in changes in mountain lion abundance within the treatment (i.e., the Bitterroot watershed, which was managed for mountain lion population reduction) or control (i.e., the upper Clark Fork watershed, which was managed for a stable mountain lion population) areas. To address our second objective, we developed an integrated elk population model to estimate *per capita* recruitment rate (i.e., the product of fecundity and calf survival from parturition through the first year, hereafter recruitment) and population growth rate in elk populations within the mountain lion harvest treatment area and control area. We then compared time series trends in *per capita* calf recruitment and population growth during the 5 years before and after mountain lion harvest treatment to evaluate the strength of evidence for a change in population-level vital rates.

STUDY AREA

We conducted the study in the southern Bitterroot watershed located primarily in Ravalli County (Bitterroot) and the Rock Creek and Flint Creek portions of the upper Clark Fork watershed located primarily in Granite County in west-central Montana (Clark Fork; Fig. 1). The Bitterroot study area was located within a watershed managed for mountain lion population reduction (i.e., treatment area), and the Clark Fork study area was within a watershed managed for stable mountain lion

abundance (i.e., control area). The Bitterroot study area spanned portions of elk hunting districts (HDs) 250 and 270 and mountain lion management units (LMUs) 250 and 270. Elevations ranged from 1,200 m to 2,600 m, with moderate to steep terrain. Precipitation ranged annually from 40 cm in the valley bottoms to 88 cm in the mountains, and primarily fell as snow during winter (PRISM Climate Group 2013). The Clark Fork study area spanned portions of elk HDs 210, 211, 212, 213, 214, 215, and 216 and LMUs 210, 211/216, 212/215, and 213/214. Elevations ranged from 1,095 m to 2,753 m, with moderate to steep terrain. Precipitation ranged annually from 31 cm in the valley bottoms to 113 cm in the mountains and primarily fell as snow during winter (PRISM Climate Group 2013). Ungulate species in both study areas included elk, white-tailed deer (*Odocoileus virginianus*), mule deer, bighorn sheep (*Ovis canadensis*), and moose. In addition to mountain lions, large carnivore species occurring during this study included gray wolves and black bears.

Elk and Mountain Lion Harvest Background

Mountain lion harvest quotas, and presumably population size, have varied during the past 20 years in management units within our study area (Appendix A). From 2009–2011, the 3 years prior to implementation of new harvest regulations, harvest within the 2 Bitterroot LMUs averaged 12.3 (SD = 4.0) mountain lions (9.3 male and 3.0 female over 3,335 km²) annually. From 2009–2011, harvest within the 4 Clark Fork LMUs averaged 9.0 (SD = 2.7) mountain lions (7.6 male and 1.3 female over 6,881 km²) annually. In February 2012, the Montana Fish and Wildlife Commission adopted mountain lion harvest management changes for west-central Montana. The goals of management were to achieve sufficient mountain lion harvest, particularly harvest of females to reduce abundance across

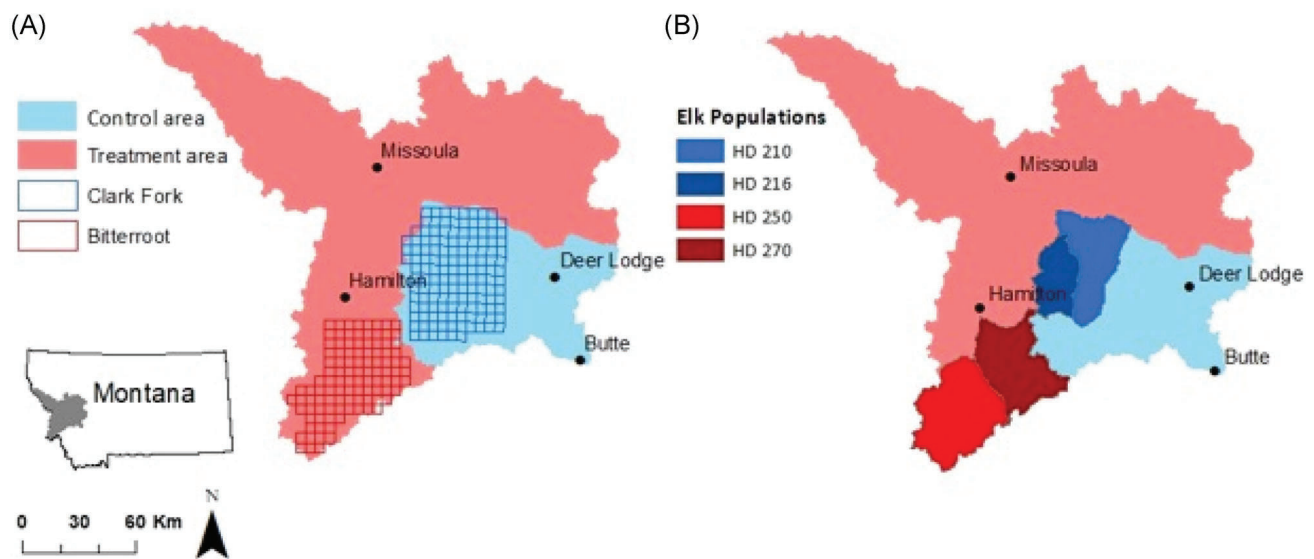


Figure 1. We conducted a carnivore-ungulate management study in west-central Montana, USA. The Bitterroot study area was located within a watershed that was treated with a mountain lion harvest management prescription designed to reduce the population by 30% (treatment area) and the Clark Fork study area was located within a watershed managed with a goal of maintaining stable mountain lion populations (control area; A). Within the Bitterroot treatment area and Clark Fork control area, we developed a 5-km × 5-km sampling grid and used spatial capture-recapture models to estimate mountain lion population abundance before and 4 years after harvest management regulations were implemented to reduce the population within the treatment area. We estimated *per capita* elk recruitment and population growth rate in 2 elk populations within the control area (HD 210, HD 216) and 2 elk populations within the treatment area (HD 250, HD 270) during the 5 years pre- and post-treatment using an integrated population model (B).

3 watersheds in west-central Montana. The management goal was an increase in mountain lion harvest intended to reduce the population by 30% to achieve short-term increases in elk calf survival and population growth rate, while also allowing for long-term mountain lion population conservation and hunting opportunity. Harvest management within the treatment area was adjusted in the third year of treatment based on lack of social tolerance for continued harvest of female mountain lions (Mitchell et al. 2018), resulting in a treatment that included a 2-year increase in female quotas (2012–2013), followed by increased male quotas (starting in 2014).

Two partially migratory elk populations occupied the Bitterroot study area: the hunt district (HD) 250 and HD 270 populations. The population in HD 250 steadily increased from approximately 600 elk in 1980 to a high of 1,300 in 2005, then steadily declined to 600–700 observed by 2009. The population in HD 270 was stable at about 1,000 from 1980 until 1998, then steadily increased to a high of 4,400 observed elk in 2013. Antlerless harvest was increased in both HD 250 and HD 270 in 2004, then restricted starting in 2007 in HD 250 and 2009 in HD 270 as elk populations declined. In HD 250, antlerless and total annual elk harvest averaged 170 (SD = 46.92) and 291 (SD = 63.25) in 2005–2007, then declined to an average of 17 (SD = 23.19) and 54 (SD = 44.49) in 2008–2017 as a result of more restrictive male and antlerless regulations implemented to reduce the effects of hunter harvest on the elk population. In HD 270, antlerless and total elk harvest averaged 458 (SD = 93.54) and 828 (SD = 187.60) in 2005–2007, then declined to an average of 100 (SD = 40.62) and 366 (SD = 48.40) in 2008–2017 as a result of more restrictive antlerless regulations implemented as part of the integrated carnivore-ungulate management program. During our study, the elk management objectives were to increase the HD 250 population towards a population objective of 1,400 and to maintain the HD 270 population at current levels given the population objective of 3,800. In Montana, state law requires Fish, Wildlife and Parks to manage elk within population objective ranges, as defined by the State Elk Management Plan (Hamlin 2004).

Two partially migratory elk populations occupied the Clark Fork study area: the HD 216 and HD 210 populations. The population in HD 216 has remained relatively stable during 2005–2017, averaging 255 observed elk. The population in HD 210 increased from 800 to 2000 observed elk during 2005–2011 and remained relatively stable at an average of 1,485 since 2011. Antlerless harvest has remained relatively stable in HD 216 and HD 210, averaging 40 and 130 per year during 2011–2017. During the study, the elk management objective was to maintain the HD 216 population at current levels given the objective of 325 observed elk and reduce the HD 210 population toward the objective of 850.

METHODS

Overview of Study Design

We estimated mountain lion population abundance in the Bitterroot treatment area and the Clark Fork control area before and after the implementation of a harvest management prescription that was designed to reduce populations in the

treatment area by 30%. We estimated mountain lion abundance in the Bitterroot treatment area at the start of the 2012 hunting season (1 Dec 2012) and again at the start of the 2016 hunting season (1 Dec 2016). We estimated abundance in the Clark Fork control area at the start of the 2013 hunting season and again at the start of the 2017 hunting season. We used a multi-strata, spatial capture-recapture model to estimate Bitterroot and Clark Fork area population abundances and test for changes in abundance before and after the harvest treatment. We predicted that if the prescribed harvest treatment was effective in achieving the targeted harvest, mountain lion population abundance in the Bitterroot treatment area would be lower post-treatment than pre-treatment, and abundance in the Clark Fork control area would remain the same pre-and post-treatment.

We also estimated recruitment and population growth rates during the 5 years before and 5 years after implementation of the mountain lion treatment in 2 elk populations within the treatment area and 2 populations within the control area. We collected annual count, age and sex classification, and harvest data from 2006–2017 for these 4 elk populations and estimated *per capita* elk recruitment and population growth rate annually for each population using an integrated population modeling approach. We then tested for changes in trends in *per capita* recruitment and population growth rate by explicitly estimating the difference between the trend(s) for these vital rates during the 5 years before (2006–2011) and after (2013–2017) mountain lion harvest treatment. We predicted that if the mountain lion harvest treatment was effective in increasing elk calf survival, recruitment rates would be greater in the treatment area during post-treatment than during pre-treatment and remain the same pre-and post-treatment in the control area. We also predicted that if changes in recruitment rates were biologically meaningful drivers of elk population growth, growth rate would be greater post-treatment than pre-treatment in the treatment area and remain the same pre-and post-treatment in the control area.

Mountain Lion Sampling and Data Collection

We estimated the abundance of independent-aged mountain lions at the start of winter (1 Dec) using recent advances in spatial capture-recapture modeling (SCR; Royle et al. 2013). We overlaid a 5-km × 5-km grid across each study area and started search effort each day in a randomly assigned grid cell. We stratified the starting location in this manner to ensure sampling was allocated across both the high- and low-quality habitat as quantified by a mountain lion resource selection function model (Robinson et al. 2015). We used a spatially unstructured sampling design wherein samples resulted from direct search effort by hound handlers (Russell et al. 2012, Proffitt et al. 2015). Hound handlers and trackers searched for mountain lion tracks, and opportunistically collected hair and scat samples along search routes. When a fresh track was located, the handler released trained hounds to locate and tree the mountain lion. We collected muscle samples from treed mountain lions using biopsy darts fired from a carbon dioxide-powered rifle (Palmer Cap-Chur, Powder Springs, GA, USA; University of Montana Institutional Animal Care and Use Committee [IACUC] 027-11MHWB-042611). We inspected

tracks to determine if the mountain lion was independent or associated with a family group, and recorded group size. We estimated age class and sex to determine which member of the group was the mother or potential offspring (we determined actual sex and relatedness based on DNA analysis). All field teams used a global positioning system (GPS) to record the length (in km) and location of their search effort for inclusion as a covariate affecting SCR models.

Harvest and management removals occurred during the sampling period, and we included samples collected from animals that were harvested within the study area. In Montana, the hide and skull of each mountain lion harvested must be presented to Montana Department of Fish, Wildlife and Parks. During the mandatory check, officers collected a muscle sample from each harvested animal. We also used information from the mandatory check to track annual harvest of male and female mountain lions within the study areas.

We radiocollared a sample of mountain lions in the Bitterroot and Clark Fork study areas to inform development of SCR models (Sollmann et al. 2013). We targeted an equal sample of males and females in each quadrant of each study area (i.e., the NW, NE, SW, and SE portion of each trapping grid) for collaring. When we treed an adult mountain lion in an area suitable for capture, we chemically immobilized the animal and outfitted it with an eartag and GPS radio-collar (Telonics style TGW-4477-4, Telonics telemetry-electronics Consultants, AZ, USA) in compliance with Montana State University IACUC permit 2016-6. We programmed collars to collect 6 locations per day, upload locations daily through the Iridium satellite system, and drop-off the animal 24 months after deployment. We censored the dataset to include only locations estimated from 3-dimensional satellite fixes. We randomly selected 1 location per animal per day for each day of the study period (1 Dec–15 Apr) for inclusion in the space-use component of the SCR model to approximate a temporal series of independent locations (Royle et al. 2013).

DNA Analysis

We performed genetic analysis of hair, scat, and muscle samples to identify the sex and individual identity of sampled mountain lions following methods described in Biek et al. (2006), Russell et al. (2012), and Proffitt et al. (2015). We genotyped tissue samples using 20 variable microsatellite loci used previously for mountain lions and ran samples a total of 4 times to detect inconsistencies between amplifications. We tested the relatedness of individuals whose samples were collected from animals encountered as part of a potential family group. If animals were related based on DNA analyses and field identified as an adult female and subadult(s) that were traveling together, we censored the subadult(s) and included only the adult female. This removed dependent offspring traveling with their mother from the dataset. If animals were related based on DNA and both were field identified as subadults that were traveling together, we included both subadult siblings in the analysis because we considered these animals to be independent. Therefore, our abundance estimates included only independent animals. After identifying individuals, we assessed spatial locations to identify high-leverage individuals, and censored all but

the last location of high-leverage individuals (available online in Supporting Information). We censored high-leverage individuals to ensure that space-use parameters reflected only the common space-use patterns of animals and to avoid bias induced in abundance estimates.

Spatial Capture-Recapture Modeling

We developed a multi-strata SCR model to estimate the abundance of mountain lions in each of our 2 study areas during both the pre- and post-treatment sampling periods based on previous work using similar models in this system (Sollmann et al. 2013, Paterson et al. 2019a). We defined the state space for the SCR model as the study area buffered by 12.5 km based on previous work indicating this extent would capture animal movement within the trapping grid (Proffitt et al. 2015). There are 3 main components of our SCR model: a model for the distribution of animal activity centers in space, a model for the probability of encounter given activity centers, and a model for the telemetry information.

The SCR model component for the distribution of animal activity centers in space included a covariate representing a separately estimated mountain lion resource selection function (RSF; Robinson et al. 2015). Previous work suggested this RSF was a strong predictor of activity centers (Proffitt et al. 2015, Paterson et al. 2019a). The RSF predicted the relative probability of mountain lion use during winter (1 Dec–15 Apr) and was developed based on GPS location data from 85 independent-aged collared male and female mountain lions from 9 different study areas in Montana (Robinson et al. 2015). The RSF included 9 variables representing terrain, land cover, and distance from forests, and validated well on both training and testing data. Accordingly, we divided the state space into a grid of cells; we then assigned each cell the mean value of the underlying RSF. We used a 4-km \times 4-km cell size for each cell in the state space. The purpose of the state-space grid is to approximate the underlying density surface of animal activity centers; preliminary model runs suggested that estimates stabilized at this resolution while keeping computation times tractable. The first component of our model expressed the expected number of activity centers in each state-space cell as a function of the RSF value on the log scale:

$$\log(\mu(s, \beta)) = \beta_0 + \beta_{RSF} \text{RSF}(s), \quad (1)$$

where $\mu(s, \beta)$ is the expected number of activity centers in state-space cell s given the covariate value $\text{RSF}(s)$ and regression coefficients β_0 and β_{RSF} .

We defined our observation process using the bivariate-normal model to define how the probability of detecting individual i in trapping cell j on occasion t decays with the distance from the location of an individual's activity center (s_i) to the center of a trapping cell (x_j) such that the probability of observation was:

$$p_{i,j,t} = p_{ijt}^0 \exp\left(\frac{-1}{2\sigma_{sex}^2} \times d(x_j, s_i)^2\right), \quad (2)$$

where p_{ijt}^0 was the probability of detection when the distance between an individual's activity center and the trap was zero

($d(x_j, s_i) = 0$), and σ_{sex} was a sex-specific scale parameter that regulates how the probability of detection declines with distance. We defined p_{ijt}^0 on the logit scale:

$$\text{logit}(p_{ijt}^0) = \alpha + \beta_{sex}(\text{Sex}_i) + \beta_{effort} \times \log(\text{effort}_{j,t}), \quad (3)$$

where α was the baseline detection probability, Sex_i is an indicator variable (female = 0, male = 1), and $\text{effort}_{j,t}$ is the effort expended in cell j during occasion t . We set p_{ijt}^0 to zero for any trapping cell in which no effort was expended. We included the locations of harvested individuals as if they arose from the detection process; previous work has suggested this introduces negligible bias into estimates (Paterson et al. 2019a) and can improve SCR-based estimates of abundance (Proffitt et al. 2015). We censored these animals from the model for all occasions following harvest to avoid a bias in detection probabilities and violating the population closure assumption.

Finally, we defined the telemetry model as a multinomial process where the vector of daily locations for animal i given an activity center s_i , m_i , was governed by an underlying model of space use that shared the space-use parameters with the observation model

$$m_i \sim \text{Multinomial}(R_i, \pi_i), \quad (4)$$

where R_i is the total number of fixes for individual i , and π_i is the vector of probabilities where each component of the vector is represented by a state-space cell and is defined as:

$$\pi_{i,j} = \frac{\exp\left(\frac{-1}{2\sigma_{sex}^2} \times d(x_j, s_i)\right)}{\sum_{j=1}^S \exp\left(\frac{-1}{2\sigma_{sex}^2} \times d(x_j, s_i)\right)}, \quad (5)$$

where S is the total number of state-space cells in the study area.

We predicted that sharing information across time and space would improve inference of abundance, and we tested this prediction by comparing inference from the 4 competing multi-strata models that allowed different amounts of information in baseline detection (α) and space-use parameters (σ_{sex}^2) to be shared (Table 1). We did not allow information sharing when estimating the effort effect on detection because we assumed this was specific to each study area and year. Similarly, we did not allow information sharing when estimating the RSF effect on the probability of an activity center because we assumed this

relationship was specific to each study area and year given its relationship with abundance (Proffitt et al. 2015).

Bayesian Analysis of SCR Models

We constructed our SCR model using a data-augmentation approach (Royle et al. 2013). This method adds a number of all-zero capture histories to the observed data and estimates the proportion of these augmented histories that are real. We added 300 unencountered animals to each of the 4 SCR datasets, a number that was large enough to ensure the resulting estimates were not bounded by our choice. To complete the model specification, we assigned diffuse priors for the remaining parameters: we gave space-use parameters (σ^2) uniform $U(0, 10)$ priors, detection parameters on the logit scale and abundance parameters on the log scale normal $N(0, 1)$ priors, and sex ratio parameters (ψ_{sex}) uniform $U(0, 1)$ priors. We estimated model parameters via Bayesian Markov chain Monte Carlo (MCMC) methods using the NIMBLE programming language (code available online in Supporting Information; de Valpine et al. 2017) within the R environment (R Core Team 2017). This approach allowed us to customize the sampling algorithms for efficiency and to use custom functions to marginalize over the discrete latent state that was the activity center for un-encountered animals, a technique that greatly improved speed. We ran models using 2 chains, each with 30,000 iterations. We discarded the first 10,000 iterations as burn-in, and thinned chains by keeping every second sample, which resulted in 20,000 samples in the approximate posterior distribution. We graphically assessed convergence using traceplots (Gelman and Hill 2007).

To estimate the sex-specific abundances of mountain lions over the state space, study areas (i.e., trapping grids), and management areas of interest, we used the estimated relationship between the underlying RSF and number of activity centers (i.e., eq. 1) to predict the number of activity centers for each state-space pixel. To derive abundance estimates, we summed the expected values for all state-space cells that fell within each area of interest and then applied the estimated sex ratio for each study area and year combination to estimate the number of males and females. Finally, because each of these abundance estimates is space specific, we calculated abundances as the estimated number of individuals divided by the area of the state space.

We evaluated the goodness of fit for the SCR models using a posterior predictive check (Gelman and Shalizi 2011, Royle et al. 2013). Our biological inference was particularly focused on

Table 1. Competing multi-strata spatial capture-recapture models estimating mountain lion spatial abundances within the Bitterroot and Clark Fork study areas in west-central Montana, USA, during 2 time periods corresponding to different mountain lion harvest management prescriptions. Competing models shared different combinations of information on baseline detection probability (α) and sex-specific space use (σ_{sex}^2) across study areas and time periods.

Model	Model description	Model formulation
1	Baseline detection shared within study areas only; sex-specific space use shared within study areas only	Shared within study area: α Shared within study areas: $\sigma_{male}^2, \sigma_{female}^2$
2	Baseline detection shared within study areas only; sex-specific space use shared across study areas	Shared within study area: α Shared across both study areas: $\sigma_{male}^2, \sigma_{female}^2$
3	Baseline detection shared across study areas; sex-specific space use shared within study areas only	Shared across both study areas: α Shared within study areas: $\sigma_{male}^2, \sigma_{female}^2$
4	Baseline detection shared across study areas; sex-specific space use shared across study areas	Shared across both study areas: α Shared across both study areas: $\sigma_{male}^2, \sigma_{female}^2$

estimating the number of males and females, given the sex-specific harvest quota system and prior work suggesting that space use and detection differed between the sexes (Proffitt et al. 2015). We therefore compared the observed number of males and females in each study area and year to the posterior distribution of the expected number of individuals seen at least once in datasets that were replicated from the posterior distribution of model parameters. We calculated a 1-sided Bayesian P -value as the proportion of MCMC samples where the expected value was greater than the observed value. If the model fit was sufficient, we evaluated changes in mountain lion abundance by comparing the estimated sex-specific abundances and ratios from the model.

Elk Population Model

To assess changes in the population dynamics of elk herds in both study areas, we used an integrated population modeling approach (Paterson et al. 2019b) that models 2 separate processes: 1) the biological processes of survival, *per capita* recruitment, and harvest, and 2) the observation process that gives rise to the observed counts and age ratios. We used annual spring count and age-sex classification data collected from fixed wing aircraft. Surveys were conducted annually on the winter range for each hunting district in the late spring prior to the migration to summer range and the birth pulse as part of routine population monitoring. In each district-year observers did not classify all counted animals according to age-sex class; therefore, the number of animals in each age and sex classification represented a sample of the total number of animals that were counted. Not every district had count and age-sex classification data for each of the years (2006–2017), which generated a discontinuous time series. We treated the age-sex classifications in these years as missing data.

We defined the annual population cycle from the birth pulse (May–Jun) through the following spring (Mar–Apr) when calves recruit to the population as 1-year-olds. The population cycle can be represented as an age-structured matrix model, where the expected number of calves ($E(N_{t,u}^c)$), adult females ($E(N_{t,u}^{af})$), and adult males ($E(N_{t,u}^{am})$) in year t and unit u is given as:

$$E \begin{Bmatrix} N_{t,u}^c \\ N_{t,u}^{af} \\ N_{t,u}^{am} \end{Bmatrix} = \begin{Bmatrix} \tau N_{t-1,u}^{af} - h_{t,u}^c \\ \phi_a (\delta N_{t-1,u}^c + N_{t-1,u}^{af} - h_{t,u}^{af}) \\ \phi_a ((1 - \delta) N_{t-1,u}^c + N_{t-1,u}^{am} - h_{t,u}^{am}) \end{Bmatrix}, \quad (6)$$

where the vital rates that connect the population size across years are adult survival (ϕ_a , estimated from the model), the proportion of calves that were female (δ , here assumed to 0.5), and the *per capita* recruitment rate (τ , estimated from the model), and h^c , h^{af} , and h^{am} are age and sex-specific harvest levels. We derived estimates of year-specific λ by summing the estimated abundances of each age class in year t and dividing by the sum of the estimated abundances of each class in year $t - 1$.

We used a Poisson distribution to incorporate demographic stochasticity. We treated the number of adult females in year t and unit u as a realization from a Poisson process with a

mean equal to the expected number from the matrix model above:

$$N_{t,u}^{af} \sim \text{Poisson}(\phi_a (\delta N_{t-1,u}^c + N_{t-1,u}^{af} - h_{t,u}^{af})). \quad (7)$$

We treated the number of animals recruiting into the population as a function of the number of females in the previous year and the *per capita* recruitment rate:

$$N_{t,u}^c \sim \text{Poisson}(\tau N_{t-1,u}^{af} - h_{t,u}^c). \quad (8)$$

We assumed the proportion of calves that were female was 0.5 (Eacker et al. 2016, Forzley 2019).

We modeled the observation process to accommodate the specific structure of the survey data available for these populations. Unlike in previous studies (Eacker et al. 2017) that assumed independent counts of age and sex classes, these data typically included only a single count for the total population size and an age-sex classification that was based on a sample from that total count. We first modeled the total count of all elk as an overdispersed Poisson random variable with the mean equal to the unknown (latent) true population size:

$$\text{Count}_{t,u}^{\text{total}} \sim \text{Poisson}(N_{t,u}^{\text{total}} e^{\epsilon_{t,u}}), \quad (9)$$

where $N_{t,u}^{\text{total}} = N_{t,u}^{\text{am}} + N_{t,u}^{af} + N_{t,u}^c$, and $\epsilon_{t,u} \sim \text{Normal}(0, \sigma^2)$ is an observation-level random effect to account for overdispersion, or extra variation around the count beyond what is captured by the dispersion term in the Poisson distribution. Our approach coupled a biased observation process (counts as an underestimate of the true population) to an unbiased population model that incorporates harvest. Inference regarding variation in vital rates, particularly population growth rates and fecundity, is robust to this conflation (Nilsen and Strand 2018) even as imperfect detection biases estimates of true population size, provided that observation error from year to year is essentially random (Kéry and Schaub 2011).

We used a multinomial distribution to connect the total number of animals classified ($\text{Classified}_{t,u}$) to the classified number of calves (Count^c), adult females (Count^{af}), and adult males (Count^{am}):

$$[\text{Count}^c, \text{Count}^{af}, \text{Count}^{am}]_{t,u} \sim \text{Multinomial}(\boldsymbol{\pi}_{t,u}, \text{Classified}_{t,u}). \quad (10)$$

We further assume that the observed count of calves, adult females, and adult males are proportional to their representation in the underlying population:

$$\boldsymbol{\pi}_{t,u} = \left[\frac{N^c}{N^{\text{total}}}, \frac{N^{af}}{N^{\text{total}}}, \frac{N^{am}}{N^{\text{total}}} \right]_{t,u}. \quad (11)$$

Our central focus was to evaluate changes in the *per capita* recruitment rate in each study area using a segmented regression approach for a temporal trend that estimated a continuous 3-piece temporal trend: 2006–2011 (pre-mountain lion harvest treatment), 2011–2013 (during harvest treatment), and 2013–2017 (post-harvest treatment), after accounting for

bottom-up environmental (see below) and predation covariates. To further account for potential variation in population dynamics, we assessed the evidence for density dependence on offspring recruitment. We included a unit-specific relationship between the natural log of the latent population size in the previous year (i.e., $\log(N_{t-1,u}^{\text{total}})$). We modeled the *per capita* recruitment rate on the logit scale:

$$\begin{aligned} \text{logit}(\tau_{t,u}) = & \alpha_{\text{area}} + \beta_{\text{pre,area}} \times t + \beta_{\text{adjustment 1,area}} \times (t - 2011) \\ & \times I_{t>2011} + \beta_{\text{adjustment 2,area}} \times (t - 2013) \times I_{t>2013} + \zeta_t \\ & + \mathbf{x}_{t,u}\boldsymbol{\beta} + \beta_{\text{density,area}} \times \log(N_{t-1,u}^{\text{total}}), \end{aligned} \quad (12)$$

where α_{area} are area-specific intercepts, $\beta_{\text{pre,area}}$ are area-specific temporal trends for the pre-treatment period, $\beta_{\text{adjustment 1,area}}$ and $\beta_{\text{adjustment 2,area}}$ are time- and area-specific adjustments to the temporal trend, $I_{t>2011}$ and $I_{t>2013}$ are indicator variables taking the value of 1 if t exceeds the threshold (e.g., $t > 2011$ for $I_{t>2011}$) and 0 otherwise, ζ_t are mean-zero random effects for year, $\mathbf{x}_{t,u}$ is the vector of covariates corresponding to time t and hunt district u , $\boldsymbol{\beta}$ is the vector of covariate effects (see below), and $\beta_{\text{density,area}}$ corresponds to the relationship between population density and recruitment. This segmented regression model relies on adjustments to the pre-treatment slope ($\beta_{\text{pre,area}}$) based on the time t such that we could recover the actual slopes during the post-treatment period as

$$\beta_{\text{post,area}} = \beta_{\text{pre,area}} + \beta_{\text{adjustment 1,area}} + \beta_{\text{adjustment 2,area}} \quad (13)$$

Bayesian Analysis of Elk Population Model

We estimated the parameters of the population model in a Bayesian framework, a requirement given the complicated layers to the observation process. To complete the model statement, we assigned priors to each parameter. We used a Beta(1,1) prior for adult survival (ϕ_a). We assigned intercept parameters for recruitment ($\alpha_{\text{period,area}}$) uniform priors on the probability scale (Beta(1,1)) and then transformed them to the logit scale. We gave slope parameters for the temporal trend component of recruitment ($\beta_{\text{pre,area}}, \beta_{\text{adjustment 1,area}}, \beta_{\text{adjustment 2,area}}$) Normal(0,10) priors on the logit scale. We assigned parameters related to environmental or predator covariates a common regularization prior ($\boldsymbol{\beta} \sim \text{Normal}(\mathbf{0}, \sigma_{\boldsymbol{\beta}}^2)$), where $\sigma_{\boldsymbol{\beta}}^2$ was estimated from the data. Similarly, we also assigned the parameters related to density a common regularization prior ($\beta_{\text{density}} \sim \text{Normal}(\mathbf{0}, \sigma_{\beta_{\text{density}}}^2)$). We assigned initial population sizes for each unit in each year a uniform distribution that was left-truncated at the number of animals harvested in the next year, e.g., number of calves in year 1:

$$N_{1,u}^c \sim \text{Uniform}(h_{2,u}^c, 10,000). \quad (14)$$

We gave the random effects of year ($\zeta_{t,u}$) a mean-zero normal prior:

$$\zeta_{t,u} \sim \text{Normal}(0, \sigma_{\zeta}^2). \quad (15)$$

For each of the variance terms ($\sigma_{\text{obs}}^2, \sigma_{\beta_{\text{density}}}^2, \sigma_{\beta_{\text{density}}}^2, \sigma_{\zeta}^2$), we assigned a Uniform(0, 10) prior to the standard deviation.

We estimated the approximate marginal posteriors of all model parameters using the JAGS 4.3.0 program (Plummer 2003) with

the *runjags* package (Denwood 2016) as an interface in the R programming environment (R Core Team 2017). We used random initial values and ran 4 chains in parallel for both models. We graphically assessed model convergence using traceplots. We used a total of 100,000 iterations with the first 20,000 discarded from each chain, which resulted in 80,000 samples per chain in the approximate posterior distribution.

Covariates on Recruitment

Although our primary goal was to assess the strength of evidence for a change in temporal trend in *per capita* recruitment rates in the treatment and control areas, we also accounted for potentially confounding environmental factors thought to influence recruitment. We developed annual covariates for each of the 4 hunting districts to index environmental conditions during the growing season, primary productivity, winter severity, and predators.

Precipitation has been shown to have a strong influence on pregnancy rates and calf survival (Griffin et al. 2011, Proffitt et al. 2014, Foley et al. 2015). We extracted annual precipitation values for the study area from the Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, accessed 11 Sep 2018). To evaluate support for the relative importance of late spring-early summer precipitation (the lactation period) versus summer-late summer precipitation (period of increasing juvenile independence), we took the mean of all pixels in each summer range during each period to represent average early spring and summer cumulative precipitation (i.e., early spring = May–Jun, summer = Jul–Aug). We defined summer and winter ranges for each population based on aerial survey location data and generalized elk seasonal distribution maps (<http://gis-mtftpw.opendata.arcgis.com/>, accessed 1 Feb 2018).

Growing season dynamics are also hypothesized to directly influence elk calf recruitment (e.g., Lukacs et al. 2018). We assumed that normalized difference vegetation index (NDVI) values derived from the moderate-resolution imaging spectroradiometer (MODIS) Terra satellite represented primary production on the landscape and served as a proxy for annual forage productivity (Pettoirelli et al. 2011). We used the 8-day surface reflectance images with 250-m resolution (MODIS product MOD09Q1) to calculate NDVI values on a per-pixel basis across the study area and through time (courtesy of the National Aeronautics and Space Administration Land Processes Distributed Active Archive Center, U.S. Geological Survey/Earth Resources Observation and Science Center, Sioux Falls, SD, USA; https://lpdaac.usgs.gov/data_access/data_pool, accessed 1 Feb 2018). We then calculated time-integrated values of NDVI for 2 periods: the start of the growing season through June, and July to the end of the growing season. We took the mean values of each metric from all of the pixels in each summer range of each herd to represent year- and herd-specific primary production.

Winter severity has also been shown to reduce elk recruitment (e.g., Christianson and Creel 2014, Lukacs et al. 2018). We used snow-water equivalent (SWE) values estimated from the Snow Data Assimilation System (SNOWDAS; National Operational Hydrologic Remote Sensing Center 2004) to

represent a metric of snowpack density on winter ranges. We calculated the cumulative SWE values for each pixel from 1 December to 31 April of each year, then estimated the mean value for each winter range as an index of winter severity.

Information on predators was available for all unit-years in our study. State regulations require that all harvested black bears be presented with intact evidence of sex, in person, to regional biologists, and those harvest numbers were available through all years and for all units in our study. End-of-the-year minimum wolf counts (number observed by 31 Dec of each year) were available as part of the state of Montana's wolf monitoring program. If wolf pack locations spanned >1 hunt district, we relied on area biologists' expertise to assign minimum numbers to each elk unit. When wolf pack territories spanned multiple elk units, we assigned the same number of wolves to each elk unit. We used the number of harvested black bears and minimum wolf counts directly as covariates in the models, assuming that the values indexed the sizes of underlying populations. We did not explicitly include information on harvested lions in our models because our goal was to understand elk population dynamics in response to the 2 mountain lion harvest regimes (i.e., pre-treatment mountain lion harvest management and post-treatment harvest management). We explicitly accounted for the effect of mountain lions in our experimental design as a blocking factor.

We calculated the pair-wise correlations between each of the covariates used in this model, and the maximum correlation was between spring precipitation and spring NDVI ($r = -0.57$). Given these modest correlations and our use of regularization priors for the coefficients of environmental variation, we proceeded to use all of the covariates in our model. We centered and standardized covariates using the mean and standard deviation prior to analysis. Finally, we included time-lagged versions of summer precipitation, summer time-integrated NDVI, and winter severity in our models, corresponding to conditions experienced by adult female elk in the summer prior to conception and the winter when the calf was *in utero*. We assessed the strength of evidence for a relationship between each of these covariates and recruitment by evaluating if the 90% credible interval included zero.

Elk Population Model Validation and Treatment Effects

The elk population model was a complex hierarchical model fit to datasets with large variation in observed numbers of elk, and we wanted to ensure adequate model fit prior to inference and interpretation. Similar to the SCR models for lion abundance estimation, we used posterior predictive checks to evaluate model fit (Gelman and Hill 2004, Hobbs and Hooten 2015). First, we calculated a discrepancy measure for the district- and year-specific counts to compare how well replicated datasets could capture observed variation using the Freeman-Tukey statistic:

$$T = \sum_{i=1}^N (\sqrt{\text{count}_i} - \sqrt{\text{expected count}_i})^2, \quad (16)$$

where $i = 1$ to N corresponds to the sum over all the hunting districts and years, and count_i represents the number of animals

(either observed or replicated from the model). Next, recruitment was a central focus of our work and the number of calves that were observed among years and areas had considerable variation. Therefore, our second posterior predictive check evaluated how well replicated datasets captured observed variation in calf numbers by measuring the difference between the observed and replicated variation,

$$T = \text{var}(\text{observed calves numbers}) - \text{var}(\text{replicated calf numbers}). \quad (17)$$

In both cases, we calculated 1-sided Bayesian P -values as the proportion of MCMC samples where the replicated value exceeded the observed value. Although no strict advice on the interpretation of Bayesian P -values from posterior predictive checks exists (Hooten and Hobbs 2015), models that are a poor fit to the data will have values close to 0 (indicating the model can never replicate the observed variation). In contrast, Bayesian P -values close to 0.5 indicate that the model-replicated variation exceeds observed variation as often as observed variation exceeds model-replicated variation and the model is a good fit to the data. To assess the strength of evidence for our model that included covariate effects on recruitment rates, we then compared goodness of fit to a model with no covariate effects. We considered this an additional test of whether the inclusion of environmental covariates improved inference. To assess differences in elk calf recruitment during the pre- and post-treatment periods in the treatment and control areas, we first generated the predicted relationships for the trends in each area (control and treatment) by holding environmental covariates to their median values within each area across time. These results represent a prediction of what would have happened under median environmental conditions in each area across all years. Second, we compared estimated median values of recruitment during the pre- and post-treatment periods for both areas at the level of the hunting district given the observed environmental variations during each time period. To assess differences in population growth rate during the pre- and post-treatment periods in the treatment and control areas, we predicted λ for each area given the scenario of no harvest in the previous fall and with the observed environmental variation and compared estimated median values and 90% credible intervals of λ . Next, we compared median values and 90% credible intervals of λ incorporating observed environmental variation during the pre- and post-treatment periods for both areas at the level of the hunting district.

RESULTS

Mountain Lion Harvest Management and Sampling

During the 6 years of the mountain lion population estimation study (2012–2017), the prescribed harvest quotas for males and females were mostly achieved, and management success (percent of the prescribed quota achieved) was high (Table 2). In the Bitterroot treatment area, the average prescribed male and female quotas were 3.3 males and 2.9 females/1,000 km²/year during 2012–2017, and the average achieved harvest was 3.0 (SD = 0.6) males and 2.5 (SD = 1.3) females/1,000 km²/year. The average male and female harvest management success in the

Table 2. The male and female mountain lion prescribed harvest quotas and achieved harvest for the Bitterroot and the Clark Fork study areas in west-central Montana, USA, during 2006–2017. The 3,335-km² Bitterroot study area included lion management units 250 and 270 and was managed for mountain lion population reduction (treatment area), and the 6,881-km² Clark Fork study area included lion management units 211/216, 210, 212/215/217, and 213/214 and was managed for stable mountain lion population abundance (control area). The quota and harvest per 1,000 km² is reported for comparison because the area of the Bitterroot and Clark Fork study areas differed.

Prescription type	Study area	Year	Male quota	Male harvest	Female quota	Female harvest	Male quota per 1,000 km ²	Male harvest per 1,000 km ²	Female quota per 1,000 km ²	Female harvest per 1,000 km ²
Treatment	Bitterroot	2006	7	8	0	0	2.10	2.40	0.00	0.00
Treatment	Bitterroot	2007	7	6	0	0	2.10	1.80	0.00	0.00
Treatment	Bitterroot	2008	7	2	0	0	2.10	0.60	0.00	0.00
Treatment	Bitterroot	2009	20 ^a	7	2	1	6.00 ^a	2.10	0.60	0.30
Treatment	Bitterroot	2010	30 ^a	11	4	2	9.00 ^a	3.30	1.20	0.60
Treatment	Bitterroot	2011	40 ^a	10	6	6	11.99 ^a	3.00	1.80	1.80
Treatment	Bitterroot	2012	14	12	14	15	4.20	3.60	4.20	4.50
Treatment	Bitterroot	2013	8	10	12	11	2.40	3.00	3.60	3.30
Treatment	Bitterroot	2014	10	8	7	6	3.00	2.40	2.10	1.80
Treatment	Bitterroot	2015	11	11	8	3	3.30	3.30	2.40	0.90
Treatment	Bitterroot	2016	11	7	8	8	3.30	2.10	2.40	2.40
Treatment	Bitterroot	2017	11	11	8	7	3.30	3.30	2.40	2.10
Control	Clark Fork	2006	9	4	0	0	1.31	0.58	0.00	0.00
Control	Clark Fork	2007	7	5	0	0	1.02	0.73	0.00	0.00
Control	Clark Fork	2008	7	3	0	0	1.02	0.44	0.00	0.00
Control	Clark Fork	2009	7	6	0	0	1.02	0.87	0.00	0.00
Control	Clark Fork	2010	20 ^a	8	8	2	2.91 ^a	1.16	1.16	0.29
Control	Clark Fork	2011	20 ^a	9	8	2	2.91 ^a	1.31	1.16	0.29
Control	Clark Fork	2012	20	13	3	3	2.91	1.89	0.44	0.44
Control	Clark Fork	2013	16	14	4	3	2.33	2.03	0.58	0.44
Control	Clark Fork	2014	16	13	6	4	2.33	1.89	0.87	0.58
Control	Clark Fork	2015	16	15	5	4	2.33	2.18	0.73	0.58
Control	Clark Fork	2016	16	10	5	4	2.33	1.45	0.73	0.58
Control	Clark Fork	2017	16	13	5	1	2.33	1.89	0.73	0.15

^a In some years, there was no male subquota, only a female subquota and total harvest quota. The value displayed represents the total harvest quota.

Bitterroot was 92% and 85%, respectively. In the Clark Fork control area, the average prescribed male and female quota was 2.4 males and 0.7 females/1,000 km²/year during 2012–2017, and the average achieved harvest was 1.9 (SD = 0.2) male and 0.5 (SD = 0.2) females/1,000 km²/year. The average male and female harvest management success in the Clark Fork area was 78% and 70%, respectively.

The number of sampling-days, level of search effort, number of samples included in analysis, number of individuals identified, and number of spatial recaptures varied across study areas and time periods (Table 3). The number of individuals identified and the number of spatial captures in each study area and time period, together with previous simulation-based work on the same study design, suggested that each dataset was adequate to result in unbiased spatial-capture recapture abundance estimates (Table 3; Paterson et al. 2019a).

We radio-collared a total of 15 animals (9 female, 6 male) in the Bitterroot study area and 9 (6 female, 3 male) in the Clark

Fork study area. Three individuals in the Bitterroot study area were collared over both seasons, and we treated the second season as if it were independent of the first, resulting in 18 animal-years of collar data for the Bitterroot. We included only individuals with at least 30 days of data, a filter that reduced the sample size in the Clark Fork study area to 4 females and 2 males and resulted in 6 animal-years of collar data for the Clark Fork. A total of 2,329 daily locations from 24 individuals were included in the SCR models.

Mountain Lion SCR Models

In our 4 SCR models (Table 1), which shared different amounts of information about baseline probabilities of detection and sex-specific space use, the 90% credible intervals for the β_{RSF} coefficient were consistently positive (Fig. 2). For example, model 1 predicted that abundance of activity centers in the Bitterroot study area in 2012 increased from 0.20 (90% credible interval [CrI]: CrI = 0.06, 0.35) for a state-space cell with an underlying

Table 3. The number of sampling days, search effort (in km), number of male and female samples included in analyses, the number of individual male and female mountain lions detected, average number of recaptures per individual, and average number of spatial recaptures (number of different grid cells in which an individual is captured) in the Bitterroot and Clark Fork study areas in west-central Montana, USA, during 2012–2017.

Study area	Year	Number of sampling days	Search effort (km)	Number of samples		Number of individuals detected		Average recaptures per individual	Average spatial recaptures per individual
				Female	Male	Female	Male		
Bitterroot	2012	50	8,897	50	28	37	25	1.26	1.19
Bitterroot	2016	84	14,216	41	33	33	21	1.37	1.31
Clark Fork	2013	66	12,898	37	23	21	14	1.71	1.57
Clark Fork	2017	95	10,905	39	27	25	17	1.57	1.52

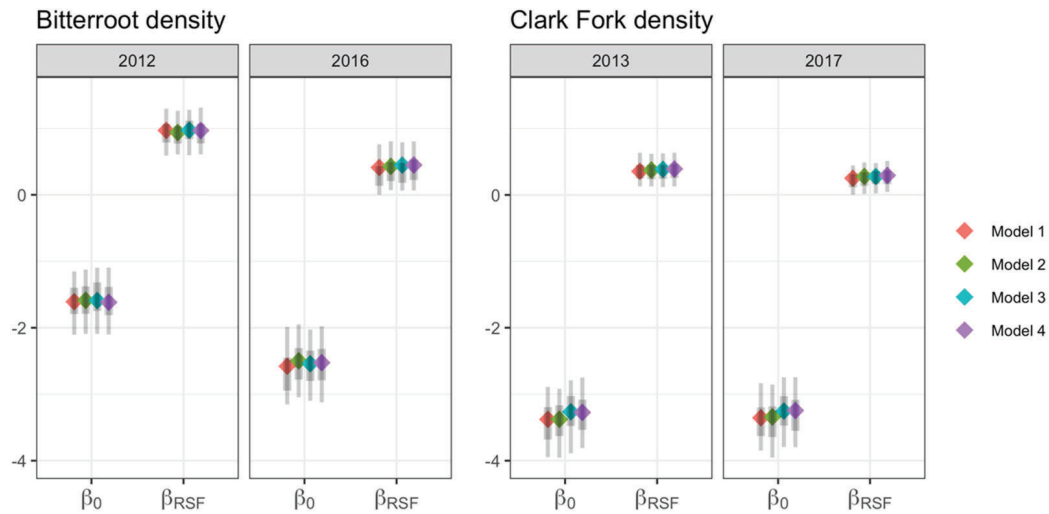


Figure 2. Coefficient estimates representing the density of animal activity centers for each of 4 competing spatial capture-recapture models estimating abundance of mountain lions in the Bitterroot and Clark Fork study areas of west-central Montana, USA, during 2012–2017. β_0 represents the overall intercept and β_{RSF} the relationship between density of activity centers and the underlying values of the mountain lion resource selection. Diamonds represent the mean of the posterior, light gray boxes the 50% credible interval, and the whiskers the 90% credible interval.

RSF value of 0.05 (the median RSF value) to 1.80 (CrI = 1.12, 2.36) for a cell with a value of 0.35 (90% quantile RSF value). We found no evidence that males had a lower overall probability of detection for the Bitterroot (2016) and Clark Fork areas (2013 and 2017), which contrasted with the Bitterroot (2012) estimates (i.e., β_{sex} did not overlap 0 in 2012; Fig. 3). In the Bitterroot in 2012, the probability of detection for 20 km of search effort (approximately the median across all years and study areas) was 0.11 (CrI = 0.07, 0.15) for females compared to 0.03 (CrI = 0.01, 0.05) for males (Fig. 3). The relationship between search effort and detection was broadly consistent across study areas and years (Fig. 3). For example, model 1 predicted the probability of detection for females in the

Bitterroot (2012) area increased from 0.11 (CrI = 0.01, 0.15) to 0.28 (CrI = 0.17, 0.38) as effort increased from 20 km to 100 km. The model-specific probabilities of detection weakly suggested that overall detection in the Clark Fork (e.g., 0.07, CrI = 0.04, 0.11 for females with 20 km of effort) was lower than in the Bitterroot (0.11, CrI = 0.07, 0.15), though overlap in the tails of the credible intervals prevented strong inference (Fig. 3).

Estimates indicated differences in space use between the sexes that depended on the model formulation used (Fig. 4). All models strongly suggested that σ_{male}^2 was higher than σ_{female}^2 in the Bitterroot (i.e., males use larger areas than females), and that σ_{male}^2 was similar among the study areas. Only models 1 and 2

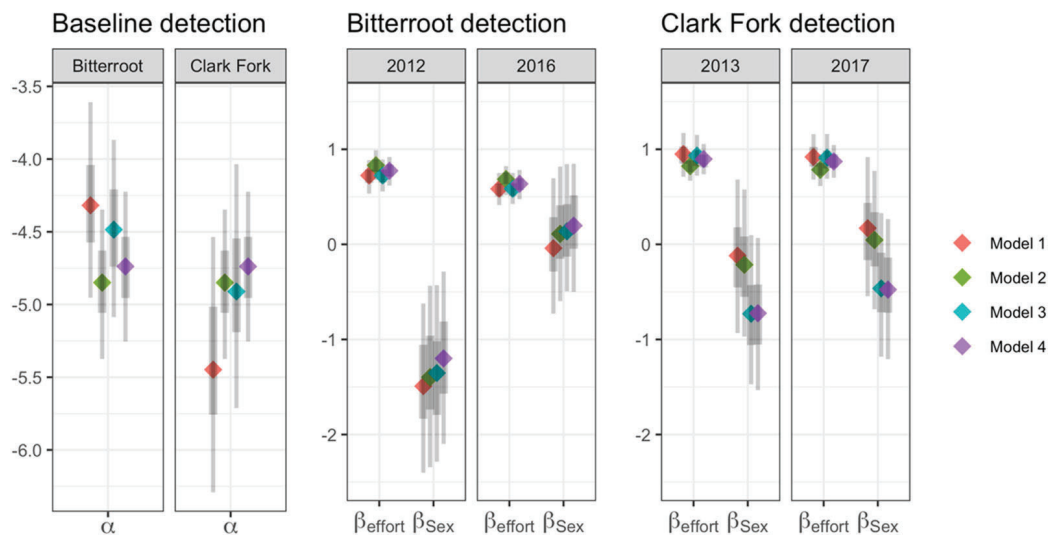


Figure 3. Coefficient estimates representing the effect of baseline detection on the logit scale (α) and the effect of search effort (β_{effort}), and sex (β_{sex}) on detection probability for each of 4 competing spatial capture-recapture models estimating abundance of mountain lions in the Bitterroot and Clark Fork study areas of west-central Montana, USA, during 2012–2017. Diamonds represent the mean of the posterior, light gray boxes the 50% credible interval, and the whiskers the 90% credible interval.

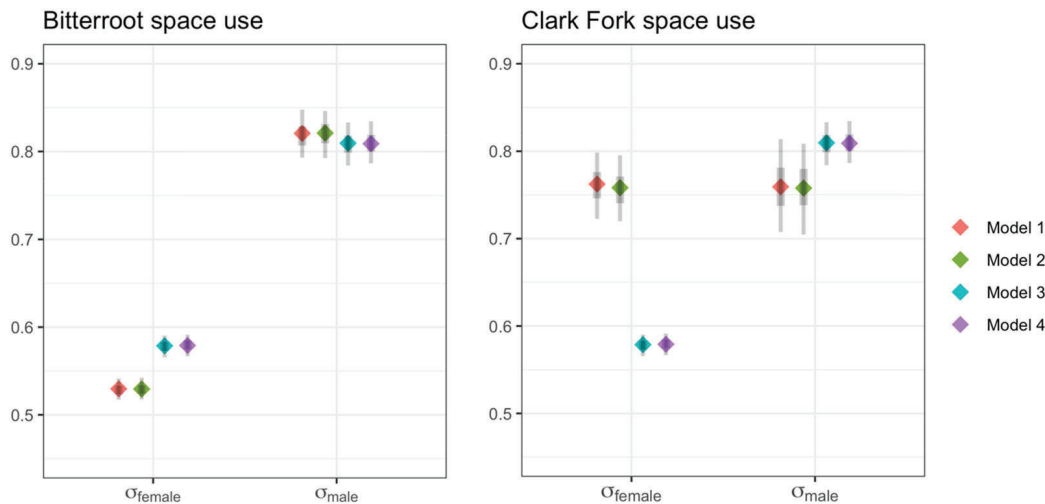


Figure 4. Coefficient estimates representing the effect of distance to an individual's activity center on female (σ_{female}) and male (σ_{male}) mountain lion probability of detection for each of 4 competing spatial capture-recapture models estimating abundance of mountain lions in the Bitterroot and Clark Fork study areas of west-central Montana, USA, during 2012–2017. Diamonds represent the mean of the posterior, light gray boxes the 50% credible interval, and the whiskers the 90% credible interval.

separately estimated sex-specific space use for each study area and indicated that females in the Clark Fork used larger areas than those in the Bitterroot, and used areas roughly equal to the size of males in the Clark Fork (Fig. 4).

There is no agreed-upon method of model selection for Bayesian models. However, the results of the goodness-of-fit metrics used to guide model selection suggested that all models adequately fit the data (Fig. S3, available online in Supporting Information). The most complex model (model 1; Table 1) suggested a lower estimated probability of detection in the Clark Fork and differences in sex-specific space use between the study areas. We chose the most complex model whose 90% credible intervals for the coefficients did not include zero (model 1). However, the resulting abundance and density estimates were similar from all 4 models (Table S2, Figs. S4–S8, available online in Supporting Information).

Pre- and Post-Treatment Mountain Lion Population Estimates

We found evidence that mountain lion abundance declined in the Bitterroot treatment area but not in the Clark Fork control area. Estimated abundance in the Bitterroot study area declined from a mean of 161 in 2012 (CrI = 104, 233) to 115 in 2016 (CrI = 69, 173). Additionally, in the Bitterroot study area we found a change in the proportion of females between 2012 (male:female = 0.50, CrI = 0.33, 0.67) and 2016 (male:female = 0.28, CrI = 0.17, 0.40). This translated into a decline in the abundance of males, and similar abundances of females (2012: males = 80, CrI = 52, 116; females = 81, CrI = 52, 117; 2016: males = 33, CrI = 20, 49; females = 82, CrI = 49, 124; Fig. 5). For the Clark Fork study area, we found evidence for a slight increase in overall abundance between 2013 (57, CrI = 37, 85) and 2017 (72, CrI = 47, 105). However, we found no

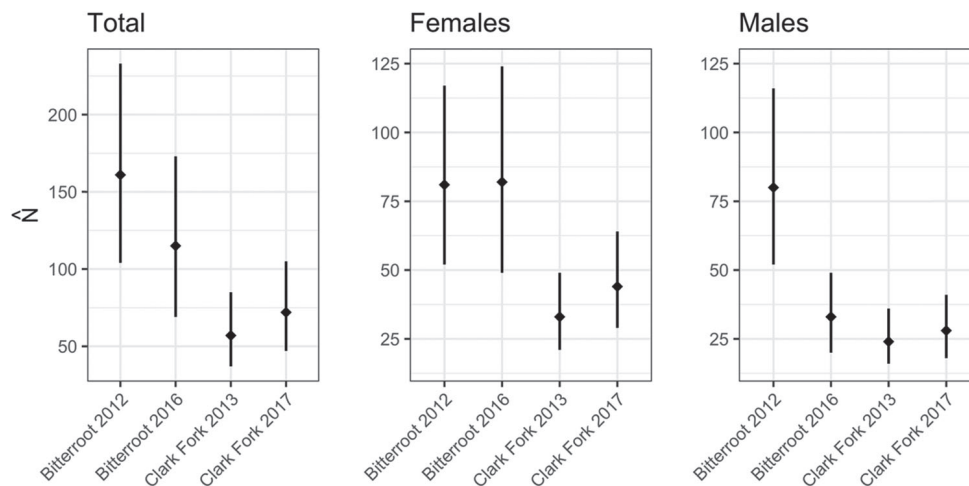


Figure 5. The total, female, and male mountain lion abundance (\hat{N}) within the Bitterroot and Clark Fork study areas of west-central Montana, USA, during 2012–2017 predicted from the most supported spatial capture-recapture model (model 1). Diamonds represent the mean of the posterior and the whiskers represent the 90% credible interval.

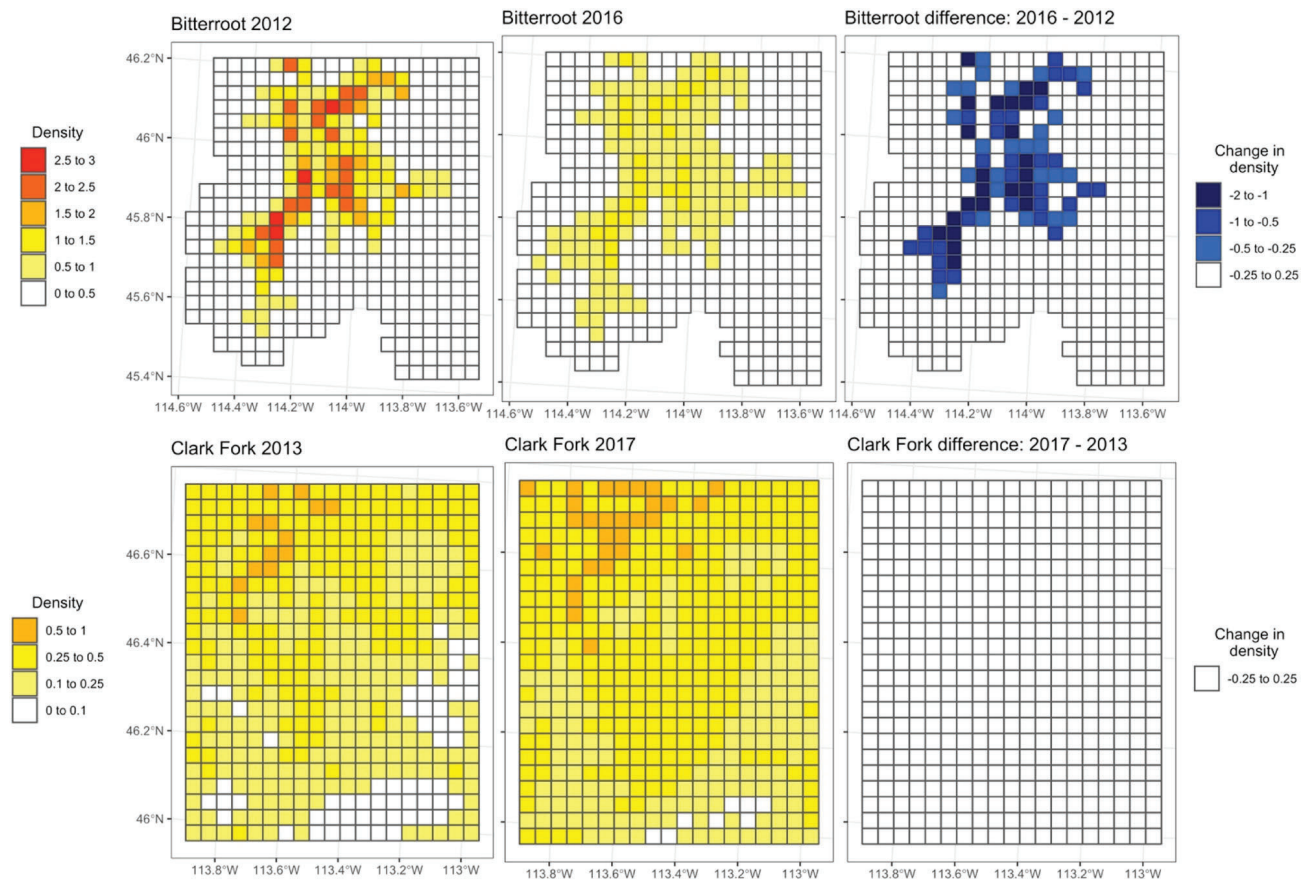


Figure 6. The predicted density and change in density per state-space grid cell of mountain lions pre- (2012, 2013) and post- (2016, 2017) harvest management treatment in the Bitterroot and Clark Fork study areas of west-central Montana, USA, estimated from the most supported spatial capture-recapture model (model 1). The third column represents the predicted changes in density between the 2 sampling periods, and the scales are the same between areas.

evidence for a change in the proportion of females between 2013 (male:female = 0.42, CrI = 0.26, 0.58) and 2017 (0.39, CrI = 0.25, 0.54). Accordingly, we obtained similar estimates of abundance of males and females between time periods (2013: males = 24, CrI = 16, 36; females = 33, CrI = 21, 49; 2017: males = 28, CrI = 18, 41; females = 44, CrI = 29, 64; Fig. 5).

Our results suggest that the relationship between abundance and the values of the underlying RSF changed over time in the treatment area. Whereas the estimated intercept (β_0) and slope terms (β_{RSF}) were roughly commensurate for the Clark Fork between 2013 and 2017 (Fig. 2), estimates for the Bitterroot differed between 2012 and 2016, which indicated that the spatial arrangement of animals on the landscape changed (Fig. 6). The more positive association between RSF values and abundance of activity centers (β_{RSF}) for the 2012 Bitterroot predicted high mountain lion abundances in cells with high RSF values, in contrast with the more moderate relationship for the 2016 Bitterroot data (Fig. 2). This change in relationship indicates that the difference in mountain lion abundance between the 2 years arose primarily from a decline in abundance for those state-space cells in the area that had the highest RSF values (Fig. 6). This contrasts the results from the Clark Fork study area, where a similar estimated relationship between RSF values and abundance of activity centers (β_{RSF}) yielded roughly similar

spatial abundances and comparatively minor differences in overall population abundance between years (Fig. 6).

Elk Data and Environmental Variation

Observed counts of elk populations demonstrated high among-hunting-district variation. In the control area, HD 210 had a mean count of 1,365 (SD = 393) over the duration of the study with a mild, apparent increase over time, and HD 216 had a mean count of 256 (SD = 107) that was approximately stable over time (Fig. 7). In the treatment area, both HD 250 (\bar{x} = 730, SD = 175) and HD 270 (\bar{x} = 3,922, SD = 363) displayed an initial decrease in counts, followed by a slow, apparent increase over time (Fig. 7). In the control area there was no obvious trend in age ratios, and the mean was roughly the same between HD 210 (\bar{x} = 25.3, SD = 2.2) and HD 216 (\bar{x} = 23.8, SD = 6.4), although HD 216 showed more among-year variation (Fig. 7). In the treatment area, observed age ratios initially decreased in both populations and reached a minimum from 2008–2009 before subsequently climbing (HD 250: \bar{x} = 21.8, SD = 9.5; HD 270: \bar{x} = 24.3, SD = 6.9; Fig. 7).

Values of the measured covariates did not display a strong temporal trend (Fig. 8; Fig. S9, available online in Supporting Information). Moreover, there was no obvious difference in the median and range of covariate values for any district between the pre- and post-treatment periods (Fig. 8).

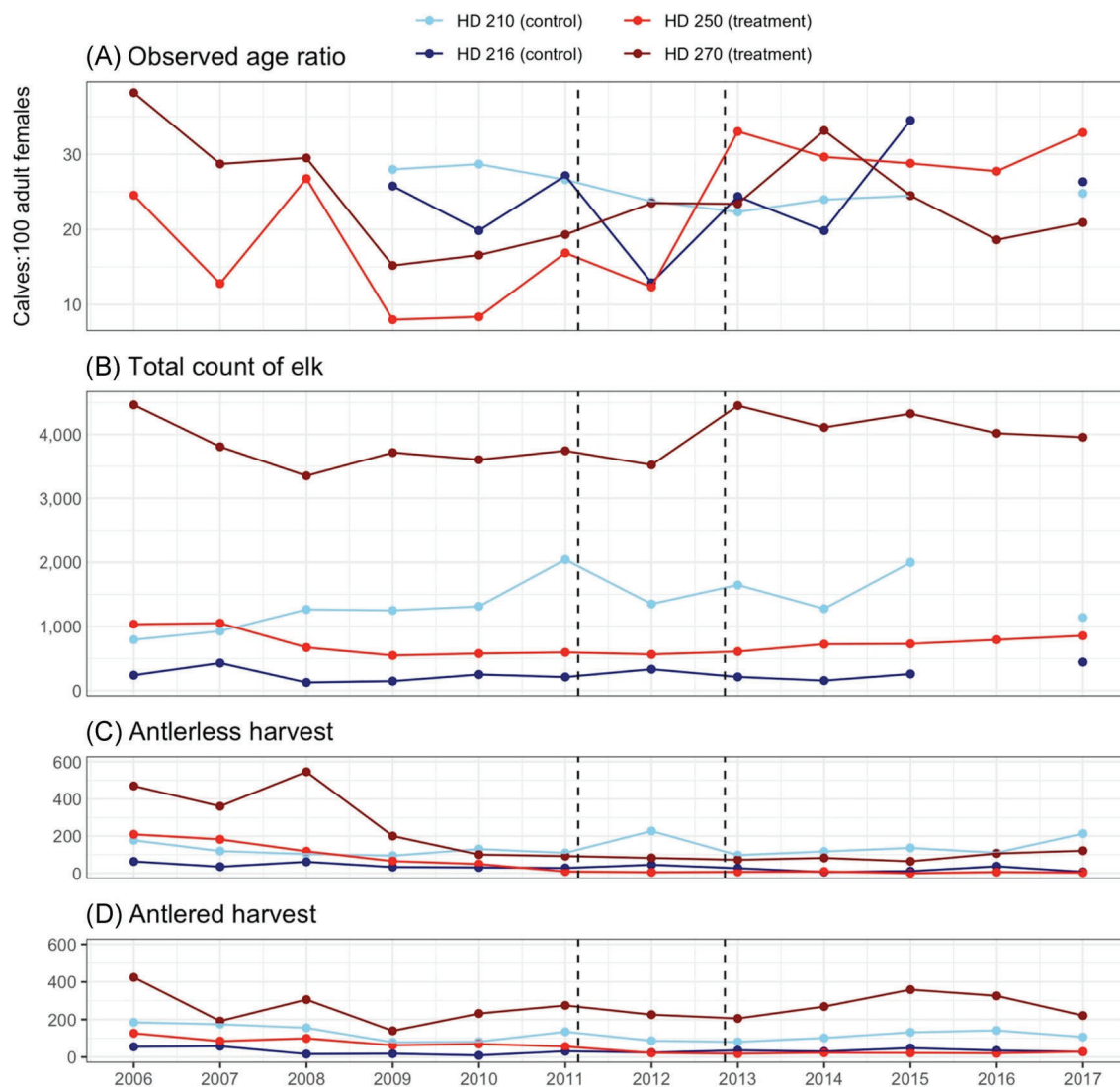


Figure 7. Summary of 2006–2017 observed age ratio (A), count (B), and harvest data (C and D) for each of the 4 elk populations in west-central Montana, USA, included in the population model. The hunting district (HD) 210 and HD 216 elk populations are located within the Clark Fork control study area and the HD 250 and HD 270 elk populations are located within the Bitterroot study area treated with a mountain lion harvest prescription designed to reduce mountain lion populations. The vertical dashed lines separate the pre-treatment era (2006–2011) from the post-treatment era (2013–2017).

Elk Population Models

The goodness-of-fit evaluations indicated that the population model adequately fit the data. The model was able to accurately replicate the variation seen in the observed count data and the variation in the number of observed calves on the ground (Figs. S10–S11, available online in Supporting Information). The null model had approximately the same goodness of fit as the model with temporal trends; consequently, we assessed the evidence for a temporal trend in the full model by examining if the credible intervals for those structural parameters included zero. We found strong evidence for the association of several environmental covariates with *per capita* recruitment rates (Fig. 9).

The median estimated recruitment rate across time and area from our model was 0.24 (CrI = 0.23, 0.26). The magnitude of bear harvest (an index of bear population abundance) had a negative relationship with recruitment, opposite to that expected if bear harvest enhanced elk recruitment and, we acknowledge, may be indicative of a potentially spurious

correlation. The estimated effect on the standardized scale was -0.26 (SD = 0.08), corresponding to recruitment declining from 0.24 for the average bear harvest of 18 to 0.20 (CrI = 0.17, 0.22) for 1 standard deviation above the average (corresponding to a total of 30 bears harvested). Cumulative SWE in the previous year had a negative relationship with recruitment as expected and had an estimated effect on the standardized scale of -0.30 (SD = 0.07), such that *per capita* recruitment declined from the overall median recruitment value of 0.24 (CrI = 0.23, 0.26) at the average SWE of 12.5 m to 0.19 (CrI = 0.17, 0.22) when SWE was 1 standard deviation above the average (corresponding to 21.2 m). We did not find a relationship with recruitment for SWE in the current year. Summer precipitation in the current year had a large, positive association with *per capita* recruitment as predicted, with an estimated effect on the standardized scale of 0.24 (SD = 0.09). This corresponded to an increase in recruitment from the overall median 0.24 (CrI = 0.23, 0.26) at the average

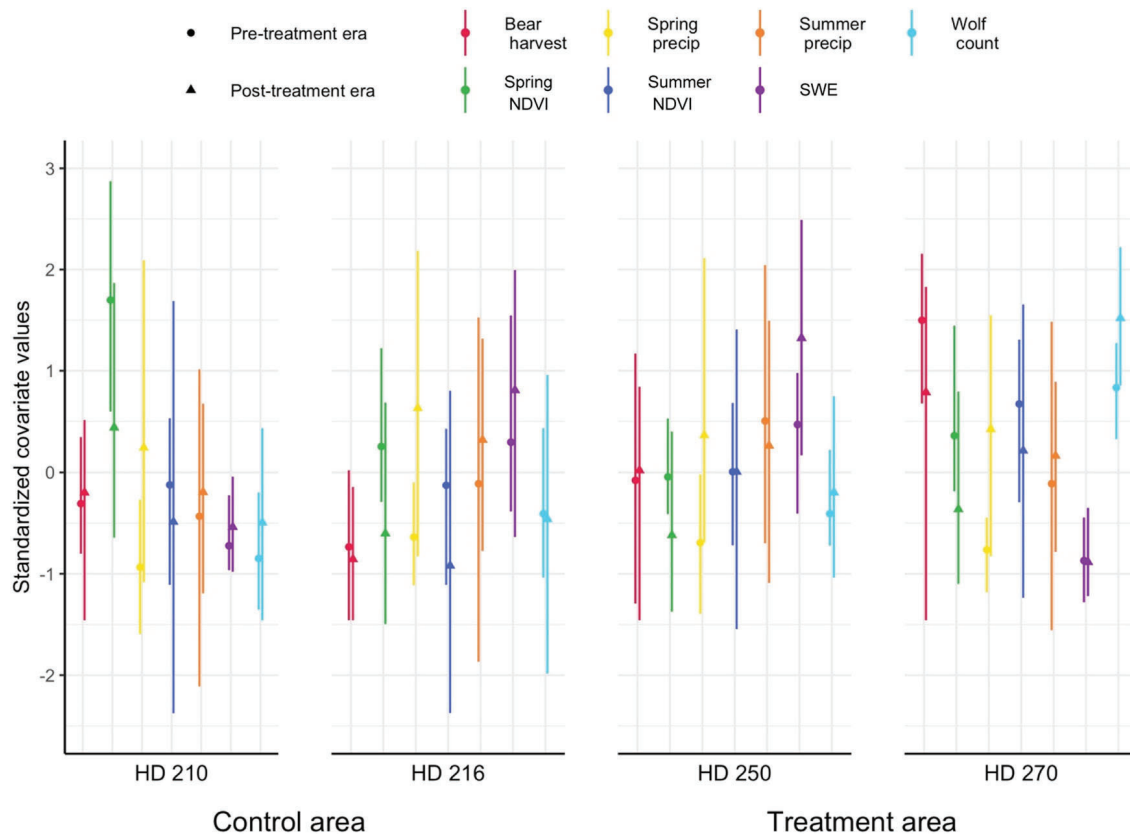


Figure 8. The median (circle = pre-treatment, triangle = post-treatment) and range (thin line) of values for covariates in the elk population model used to explain variation in *per capita* elk calf recruitment during the pre-treatment (2007–2011) and post-treatment (2013–2017) periods for 4 elk populations in west-central Montana, USA. Elk populations hunting district (HD) 210 and HD 216 were located within the Clark Fork control area, which received stable mountain lion harvest management, and the HD 250 and HD 270 elk populations were located within the Bitterroot area, which was treated with mountain lion harvest regulations designed to reduce mountain lion populations. The *y*-axis represents standardized covariate values. Covariates include indexes of predator density, seasonal integrated normalized difference vegetation index (NDVI) values, seasonal precipitation (precip), and the mean cumulative winter snow water equivalence (SWE) value for each winter range. In all cases, environmental variation is similar within units before and after the treatment period.

cumulative summer precipitation in the current year of 14 cm to 0.29 (CrI = 0.26, 0.33) when precipitation was 1 standard deviation above the average (corresponding to 17 cm). Finally, we found strong evidence for a positive association of recruitment to summer precipitation in the previous year with an estimated effect on the standardized scale of 0.17 (SD = 0.07). This corresponded to an increase in recruitment from the overall median 0.24 (CrI = 0.23, 0.26) at the average value of summer precipitation in the previous year of 12.5 cm to 0.27 (CrI = 0.24, 0.31) when precipitation was 1 standard deviation above the average (corresponding to 17 cm; Figs. S12–S15, available online in Supporting Information). We found little evidence for an association between recruitment and wolf counts, spring time-integrated NDVI, summer time-integrated NDVI, spring cumulative precipitation, or the lagged version of summer time-integrated NDVI. Finally, we found no evidence for density dependence in recruitment, measured as an association between recruitment and the size of the population in the previous year.

Pre- and Post-Treatment Elk Vital Rates

Using parameter estimates for the intercepts and slope terms from the linear trend component of the model, we first

generated the predicted relationships for the trends in each area (control and treatment) by holding environmental covariates to their median values within each area across time. These results represent a prediction of what would have happened under median environmental conditions in each area across all years (Fig. 10). We found limited evidence for a declining trend in *per capita* recruitment in the control area during the pre-treatment period (2007: median = 0.40, CrI = 0.23, 0.58; 2011: median = 0.26, CrI = 0.12, 0.39; Fig. 10). The uncertainty in these estimates and the estimated slope term ($\beta_{\text{pre,control}} = -0.15$, CrI = -0.40, 0.09) suggested an overall stable recruitment rate. Similarly, during the post-treatment period we estimated a roughly stable *per capita* recruitment rate (2013: median = 0.40, CrI = 0.26, 0.58; 2017: median = 0.25, CrI = 0.14, 0.40; $\beta_{\text{post,control}} = -0.17$, CrI = -0.36, 0.02). In contrast, we found strong evidence for a difference in temporal trends in recruitment in the treatment area. During the pre-treatment period, we estimated roughly stable *per capita* recruitment rates (2007: median = 0.21, CrI = 0.12, 0.33; 2011: median = 0.17, CrI = 0.08, 0.26; $\beta_{\text{pre,treatment}} = -0.06$, CrI = -0.28, 0.13). We found strong evidence for an initial increase in recruitment in 2013 (median = 0.42, CrI = 0.29, 0.56) followed by a steady decline ($\beta_{\text{post,treatment}} = -0.24$, CrI = -0.40, -0.09) to 2017 (median = 0.21,

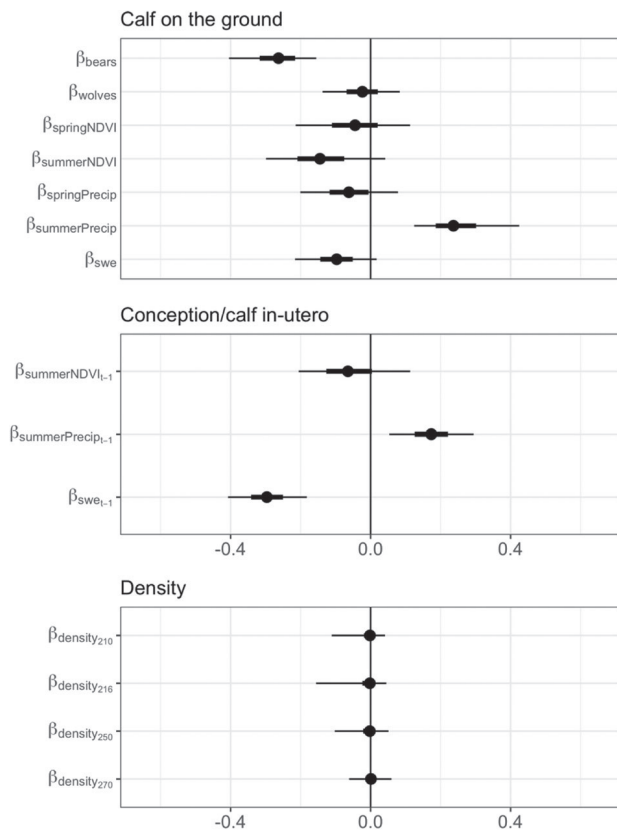


Figure 9. Estimated regression coefficients for covariates used to explain variation in *per capita* elk recruitment rate for 4 elk populations (HD 210, HD 216, HD 250, and HD 270) in west-central Montana, USA during 2012–2017 (bears = bear harvest, wolves = minimum counts, NDVI = normalized difference vegetation index, precip = precipitation, swe = snow water equivalent). The *x*-axis represents the standardized coefficient values with 0 denoted with a vertical line. Circles denote the median estimated effect, the thick line denotes the 50% highest posterior density interval (HPDI), and the thin line represents the 90% HPDI. The top panel represents covariate values during the summer or winter the calf was on the ground (i.e., following parturition), the middle panel represents covariate values that were lagged by 1 year ($t - 1$) and correspond to the year of conception and *in utero* growth (i.e., prior to parturition), and the bottom panel represents the relationship between recruitment and population density the prior year.

CrI = 0.11, 0.32), such that *per capita* recruitment rates were essentially the same in 2017 as in 2007.

Our second approach to interpreting model results regarding changes in *per capita* recruitment rates was to compare estimated median values of recruitment during the pre- and post-treatment periods for both areas at the level of the hunting district (i.e., values that incorporate the linear trend and observed environmental variation; Fig. 11). In the control area, we found that the median recruitment rates were nearly identical during the pre- (HD 210: median = 0.27, CrI = 0.23, 0.31; HD 216: median = 0.28, CrI = 0.21, 0.35) and post-treatment periods (HD 210: median = 0.26, CrI = 0.23, 0.38; HD 216: median = 0.23, CrI = 0.19, 0.28; Fig. 11). For the treatment area, we found strong evidence that the median recruitment in HD 250 increased in the post-treatment period (median = 0.33, CrI = 0.29, 0.38) relative to the pre-treatment period (median = 0.15, CrI = 0.12, 0.18) and only suggestive evidence of an increase in HD 270 (pre-treatment: median = 0.21, CrI = 0.20, 0.23; post-treatment: median = 0.28, CrI = 0.27, 0.30).

As expected, these post-treatment increases in recruitment corresponded to increases in population growth rate. Population growth rates were roughly similar in the control area during both phases, in a pattern similar to that for recruitment rates (Fig. 12). However, the estimated growth rates were influenced by changes in elk harvest in both areas through time. To aid the interpretation of the relationship between recruitment rates and growth rates while accounting for elk harvest, we predicted λ for each area given the scenario of no harvest in the previous fall and with the observed environmental variation (Fig. 13). In the treatment area, pre-treatment elk populations were declining (growth rates less than 1) from 2006–2008, and slightly increasing from 2009–2010 (e.g., 2010: $\hat{\lambda} = 1.07$, CrI = 1.04, 1.10). In a pattern similar to that found for estimates of recruitment, estimated population growth rates jumped substantially at the beginning of the post-treatment phase ($\hat{\lambda} = 1.17$, CrI = 1.13, 1.20) prior to declining to 1.06 (CrI = 1.04, 1.09) by 2017. In contrast, we found no evidence for a similar pattern or temporal trend in the control area, with population growth rates ranging from 0.87 (CrI = 0.78, 0.94) in 2015 to 1.12 (CrI = 1.08, 1.17) in 2014.

The conclusion from this approach to disentangling elk harvest from population growth rates was supported by a simple comparison of estimated population growth rates incorporating harvest in the final 3 years of the pre-treatment phase and first 3 years of the post-treatment phase, when harvest in each district was relatively stable (Fig. 7). In the treatment area, the 3-year arithmetic mean growth rate for the final 3 years of the pre-treatment period was 1.05 (CrI = 1.00, 1.10), and the 3-year mean growth rate for the first 3 years of the post-treatment period was 1.14 (CrI = 1.05, 1.21). In the control area, the 3-year mean growth rate for the final 3 years of the pre-treatment period was 1.03 (CrI = 0.96, 1.09), and the 3-year mean growth rate for the first 3 years of the post-treatment period was 1.06 (CrI = 0.95, 1.15).

Finally, we compared estimated median values of λ (incorporating observed environmental variation) during the pre- and post-treatment periods for both areas at the level of the hunting district (Fig. 14). Similar to recruitment rates, in the control area we found that median population growth rates were nearly identical in the pre- (HD 210: median = 1.01, CrI = 0.97, 1.04; HD 216: median = 0.98, CrI = 0.92, 1.05) and post-treatment phases (HD 210: median = 0.99, CrI = 0.96, 1.03; HD 216: median = 1.00, CrI = 0.91, 1.09). In contrast to the similar pre- and post-treatment estimates in the control area, we found strong evidence that median population growth rates in the treatment area were higher during the post-treatment period in HD 250 (median = 1.17, CrI = 1.13, 1.21) compared to the pre-treatment period (median = 0.84, CrI = 0.80, 0.87), and an increase in HD 270 (post-treatment: median = 1.11, CrI = 1.08, 1.13; pre-treatment: median = 1.02, CrI = 1.00, 1.04).

DISCUSSION

We found that integrated carnivore-ungulate management prescriptions achieved both the management objectives of moderately reducing mountain lion population abundance and allowing for short-term increases in elk recruitment within the treatment area. We estimated a 29% decrease in the mountain lion

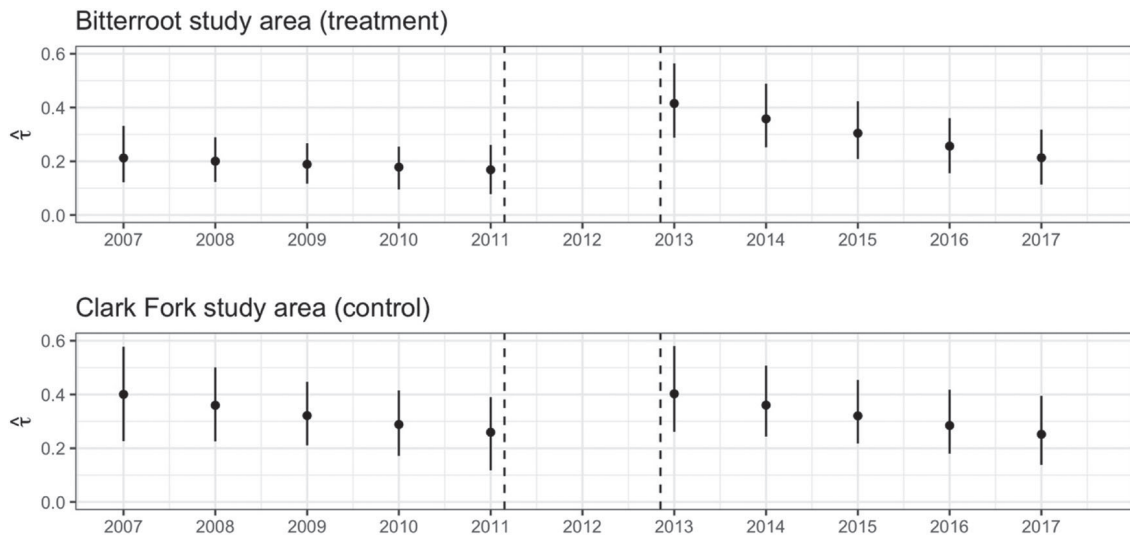


Figure 10. The spatially explicit predicted temporal trends in mean *per capita* elk recruitment rate (τ) for the Bitterroot and Clark Fork study areas west-central Montana, USA, during the 5 years pre-treatment (2007–2011) and post-treatment (2013–2017) periods assuming all elk population model covariates are held to their median values within each area across all years. The thin lines represent the 90% highest posterior density interval. The vertical dashed lines separate the pre-treatment era (2006–2011) from the post-treatment era (2013–2017).

population within the treatment area (comparing abundance prior to and 4 years after the treatment), with the greatest reductions occurring for males and within the highest quality mountain lion habitat. Following the mountain lion harvest treatment, we estimated density within the 2 hunting districts within the treatment area as 3.6 and 4.0 mountain lions/100 km² (Table S2), which indicates that long-term mountain lion conservation goals were also achieved and that a relatively high-density population persisted following the short-term harvest treatment. Elk populations within the treatment area showed increases in recruitment

rates following implementation of the mountain lion harvest treatment, although the effects on recruitment declined within 5 years. Our results indicate that management objectives to moderately reduce mountain lion populations and increase elk calf recruitment, and thus elk population growth rate, were achieved, although effects on recruitment were strongest immediately following implementation of the treatment and diminished over time.

Our results contribute to the broader body of literature regarding the effects of carnivore management on ungulate populations by providing one of the few rigorous before and after evaluation of mountain lion and elk populations using novel analytical techniques to quantify changes in both populations relative to a control area and support previous work that indicates large predators can limit ungulate populations. Effects of carnivore management vary widely across studies, likely because of the variability in the magnitude of carnivore harvest or removals, the unique combination of factors limiting the ungulate population under consideration, and the post-treatment monitoring approach used to draw inference (Boertje et al. 1996, Hayes et al. 2003, Hurley et al. 2011, Keech et al. 2011). In our study, there was prior evidence that mountain lion predation was a proximate limiting factor on elk calf recruitment (Eacker et al. 2016) and that elk calf recruitment was an important driver of elk population growth rate (Eacker et al. 2017). Therefore, we expected that reductions in mountain lion population abundance would result in increased elk calf survival and recruitment, and ultimately population growth rates. Concurrent work focused on elk vital rates (Forzley 2019) supports our conclusion that elk calf survival and recruitment increased following the mountain lion harvest treatment, which resulted in increased elk population growth rates.

The prescribed mountain lion harvest within the 2 hunting districts in the Bitterroot treatment study area equated to a prescribed harvest rate of 17.6% and 12.6% during the first and second year of treatment (i.e., total quotas of 28 and 20 animals

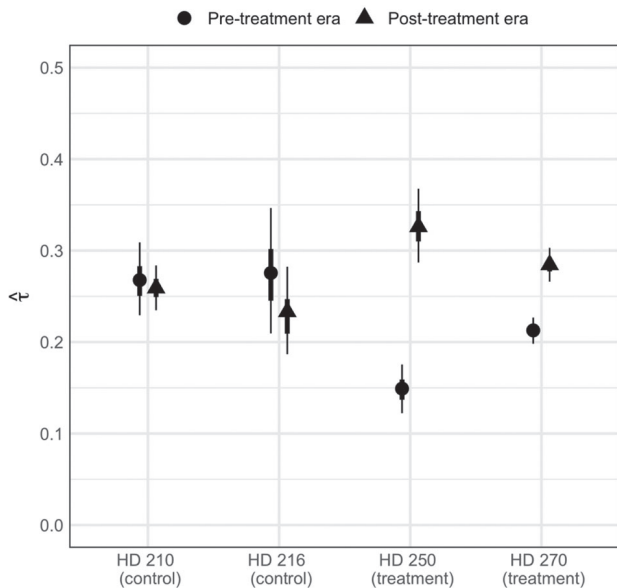


Figure 11. The estimated median *per capita* elk recruitment rates (τ) for each of the 4 elk populations categorized by hunting district (HD) during the 5 years pre-treatment (2007–2011) and post-treatment (2013–2017) west-central Montana, USA, given the observed annual covariate conditions. The symbol indicates the median, the thick line the 50% highest posterior density interval, and the thin line the 90% highest posterior density interval.

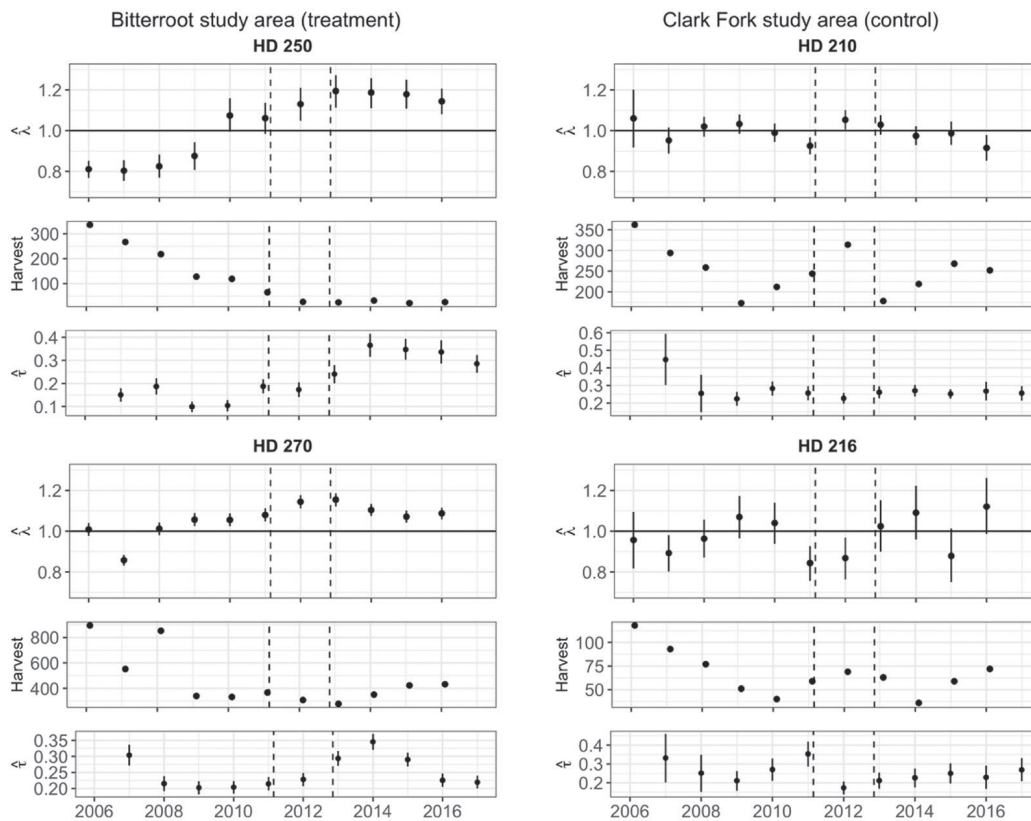


Figure 12. The estimated population growth rates (λ), total harvest, and recruitment rates (τ) for each of the 4 elk populations categorized by hunting district (HD) in the Bitterroot and Clark Fork study areas in west-central Montana, USA, during the 5 years pre-treatment (2007–2011) and post-treatment (2013–2017). Population growth rates are the aggregated result of variation in harvest and recruitment rates. The dot indicates the mean value and the thin line the 90% highest density posterior interval. The vertical dashed lines separate the pre-treatment era (2006–2011) from the post-treatment era (2013–2017).

and 159 estimated animals, Appendix F) and resulted in a 29% decrease in population abundance 4 years post-treatment. During and immediately after the treatment, the reduction may have been >29%, with a gradual recovery 3–4 years post-treatment given how resilient populations are to harvest (Ross

and Jalkotzy 1992, Robinson et al. 2014). Additionally, our results suggest that the reduction in mountain lion abundance was not uniform across the area but primarily occurred in the highest density and highest RSF value areas within the study area, potentially because hunters are more likely to target these

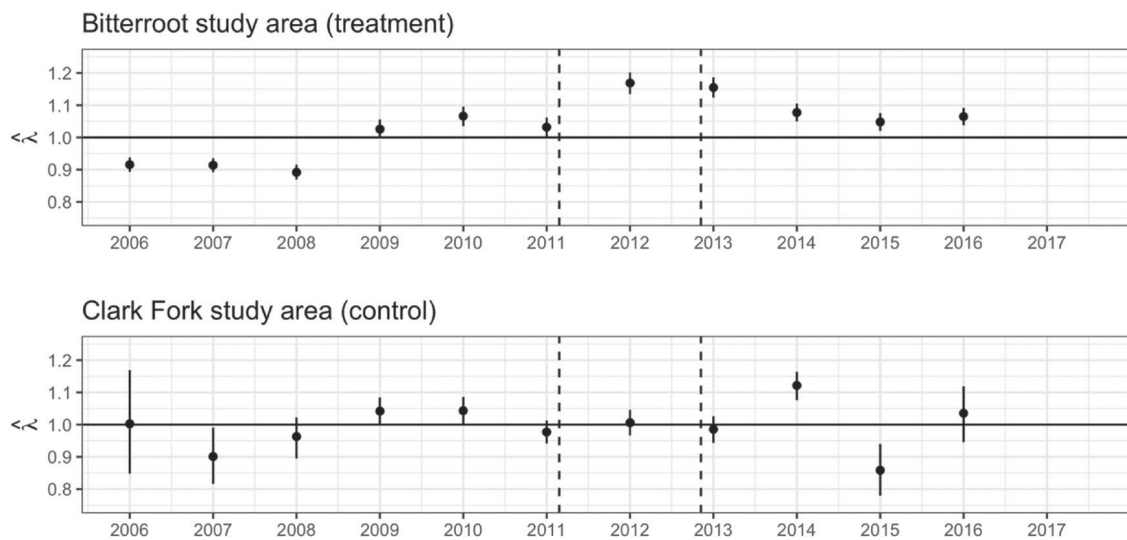


Figure 13. The predicted population growth rates (λ) for the Bitterroot and Clark Fork study areas in west-central Montana, USA, during the 5 years pre-treatment (2007–2011) and post-treatment (2013–2017) assuming no harvest the previous year. Elk populations were aggregated within each area, then λ was estimated as if there were no harvest in the previous year. The dot indicates the mean value and the thin line the 90% highest density posterior interval. The vertical dashed lines separate the pre-treatment era (2006–2011) from the post-treatment era (2013–2017).

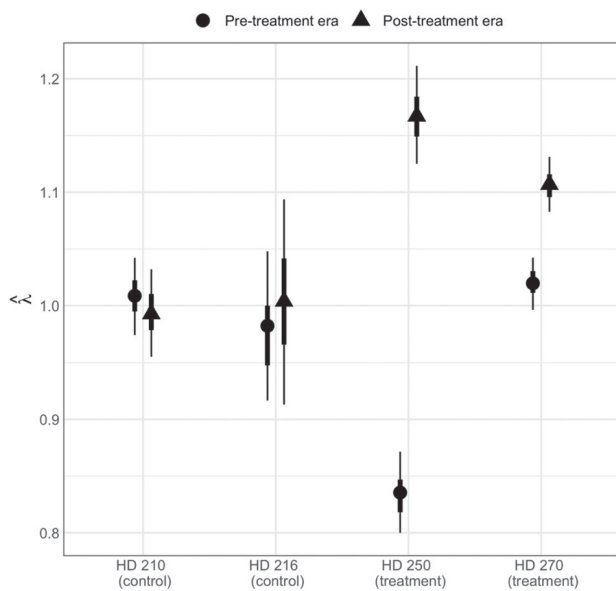


Figure 14. The estimated median population growth rates for each of the 4 elk populations categorized by hunting district (HD) in the Bitterroot and Clark Fork study areas in west-central Montana, USA, during the 5 years pre-treatment (2007–2011) and post-treatment (2013–2017) given the observed annual covariate conditions. The symbol indicates the median, the thick line the 50% highest posterior density interval, and the thin line the 90% highest posterior density interval.

areas. Although short-term increases in the female and male harvest during 2012–2014 likely contributed to the overall population reductions, the male harvest during the period between our 2 population estimates (2012–2016) was greater than the female harvest, likely contributing to the greater reduction in the male segment of the population and changes in sex ratio. Additional, longer-term monitoring of mountain lion density would be needed to estimate the duration of the effect and if population abundance increased or decreased following the cessation of the treatment.

We found that although elk calf recruitment increased following the mountain lion harvest treatment, the effects of the treatment on recruitment were short-term. Calf recruitment responds to annual variability in winter severity and growing season conditions both in our study area (Paterson et al. 2019b) and in general (Garrott et al. 2003, Griffin et al. 2011, Lukacs et al. 2018). However, even after accounting for annual and environmental variation using a population modeling approach, our dataset showed a short-term increase in recruitment following treatment (Fig. 10). These short-term effects are not unexpected, and are similar to the observed effects of increased mountain lion harvest on elk calf survival within the treatment area, which suggested elk calf survival was lowest pre-harvest treatment, highest in the first year post-treatment, and at intermediate levels 4 years post-treatment (Forzley 2019). Similarly, Hurley et al. (2011) observed only short-term effects of mountain lion and coyote reductions on mule deer populations in Idaho, USA. Mountain lion populations are capable of rapid population growth following reductions in harvest (Ross and Jalkotzy 1992, Robinson et al. 2014), and local abundance can quickly rebound to pre-treatment levels following reductions in

harvest (Robinson et al. 2014). Thus, only short-term effects on prey populations should be expected given a 2-year female harvest treatment designed to reduce populations, followed by increased male harvest. In this case, the intent of the harvest treatment was a short-term reduction in the mountain lion population that allowed for short-term release of the elk population. The diminishing effects of mountain lion harvest treatment on recruitment over time were likely due to increasing mountain lion populations following cessation of the 2-year female treatment. A promising direction for future work to more fully evaluate the implications of different management scenarios would be to couple a mountain lion population model to an elk population model, and use a simulation-based approach to understand how variation in mountain lion harvest may affect elk population trajectories.

The ability to implement carnivore harvest treatments to benefit ungulate populations is challenging given the social dynamics and controversy surrounding carnivore harvest, and public support for carnivore harvest regulations is often unknown or controversial (Decker et al. 2009, Treves 2009, Boertje et al. 2010, Mitchell et al. 2018). Decisions regarding wildlife management and harvest regulations reflect the values of a diversity of stakeholders, as well as scientific information (Riley et al. 2002). In the case of carnivore management to benefit ungulate populations, ungulate hunting advocates, carnivore hunting advocates, and anti-carnivore-hunting advocates are likely to have conflicting values that will challenge wildlife decision makers. In west-central Montana, decision-making regarding setting harvest quotas to achieve moderate mountain lion population reductions was highly controversial because of these conflicting values (Mitchell et al. 2018). The mountain lion harvest quotas prescribed to achieve a 30% reduction in mountain lion populations created controversy, with prescribed female harvest quotas being reduced following 2 years of treatment because of these controversies (Mitchell et al. 2018). Montana is a rural state with residents holding predominately utilitarian-oriented wildlife values (Teel and Manfredo 2010, Manfredo et al. 2018), yet still these harvest management decisions were highly controversial (Mitchell et al. 2018).

Elk predation from wolves within this system was likely minimal as compared to mountain lion predation (Eacker et al. 2016, Forzley 2019), and wolf predation in this system is not identified as an important factor limiting elk recruitment (Eacker et al. 2016, Forzley 2019). Additionally, wolf counts within the treatment area were stable throughout the study (Fig. 8; Appendix A) further supporting the conclusions that the observed variations in calf recruitment and population growth rate were related to changes in mountain lion population abundance and corresponding rates of predation. This result contrasts with other studies documenting important effects of wolves on ungulate populations. For example, in the Bow Valley of Banff National Park in Canada, elk population growth rate was limited by wolf predation and snow conditions (Hebblewhite et al. 2002). Similarly, in Alaska, wolf predation reduced the abundance of some moose and caribou (*Rangifer tarandus*) populations (Gasaway et al. 1992, Boertje et al. 1996). Across Idaho, wolf predation has limited adult and calf elk survival, albeit less so than mountain lion predation (Horne et al. 2019). Within the Greater

Yellowstone Ecosystem in Wyoming and Montana, USA, Garrott et al. (2005) documented that wolves had important population-level effects on one elk population with an estimated 20% of the population being killed overwinter, resulting in declining elk population trends, whereas they predicted a nearby elk population incurred only a 4% loss due to wolves, resulting in no change in the elk population trend. This variability in wolf effects on ungulate populations highlights the diversity of carnivore-ungulate relationships across systems with different carnivore and prey assemblages and densities, winter weather conditions, and primary productivity.

The effects of black bear predation on ungulate populations also vary. In our study area, previous cause-specific elk calf mortality studies suggested that black bears had only a small effect on calf survival (Eacker et al. 2016, Forzley 2019). However, in a nearby study area in Idaho, black bear predation was the primary proximate cause of calf mortality (White et al. 2010). More widely, bear predation on ungulate populations is well documented but variable (Zager and Beecham 2006, Barber-Meyer et al. 2008, Griffin et al. 2011) and can be an important limiting factor on ungulate populations in some systems (Bortje et al. 2010). Despite previous results within our study area that suggested limited effects of black bear predation on calf recruitment (Eacker et al. 2016, Forzley 2019), our elk population model provided evidence that calf recruitment was higher in areas with lower annual black bear harvest. Although bear harvest regulations were liberalized during the post-treatment era, we found no evidence that bear harvest increased (Fig. 8). Bear harvest and presumably bear population sizes were similar during the pre- and post-treatment eras (Fig. 8), and therefore it is unlikely that differences in bear harvest or harvest regulations during the pre- and post-treatment era would be responsible for the observed increases in elk calf recruitment during the post-treatment era. However, caution in interpreting these results is warranted given that the true relationship between our index of bear populations and true bear population abundances is unknown (Noyce and Garshelis 1997).

Population estimates for elusive carnivore species such as wolves, bears, or mountain lions are necessary to inform management and conservation decisions, and the methodology presented here improves the ability to monitor carnivore populations. Two advancements to previous SCR population estimation approaches are highlighted here: 1) the integration of collar location and recapture data to estimate space-use parameters (Paterson et al. 2019a), and 2) sharing of information across years and study areas using a multi-strata modeling approach. Both of these advancements are aimed at improving the precision of population abundance estimates. Additionally, recent simulation-based approaches to validation of SCR population estimates have been developed and suggest that given the capture-recapture data available in each of our 4 study area-years, our estimates of mountain lion population abundance are unbiased (Paterson et al. 2019a). These recent advances towards improving precision and detection bias in SCR population estimates increase the applicability of the SCR modeling approach and confidence in model-based population estimates generated from robust datasets such as ours.

Our SCR model selection results and estimated coefficients from our best-supported model highlight several issues that are

relevant to using SCR-based population estimation as a population monitoring tool. We found that the application of a multi-strata SCR model improved the precision of population abundance estimates, as compared to 4 independent study area-year single-season models (Proffitt et al. 2015, Morin et al. 2018). By allowing for information sharing within each study area, credible intervals around population estimates were narrower, allowing for better applicability of these models as a tool for detecting changes in population abundance. The effect of mountain lion habitat quality on the probability of activity centers being present (β_{RSF}) was consistently positive across all 4 study area-years; however, the relationship between β_{RSF} and activity centers differed between the study areas that had differences in population abundances. Although we recommend use of these methods in future studies to reduce uncertainty and improve understanding of predator-prey dynamics, this result highlights the need to be cautious in extrapolating population estimates from one study area to another, or in extrapolating study area-specific results across a broader geographical area (Boyce and McDonald 1999, Lele et al. 2013). Our results suggest that both baseline detection and sex-specific space-use parameters differed between study areas yet were similar between years within study areas. Again, this result suggests that although a multi-strata model may allow information sharing to improve parameter estimation, differences between study areas may exist, and caution should be used in sharing information across study areas. Additionally, given differences in space-use parameters between study areas, caution should be used in extrapolating results beyond the study area. Therefore, although the parameters that should be shared across studies will likely differ in each situation, we recommend that routine monitoring programs employing an SCR approach apply a multi-strata model rather than single-season model to estimate population abundances.

The elk modeling process applied in this study also offers a novel approach that provides advancements and improvements over traditional methods that have been used to interpret monitoring data. The integrated population model allowed for biological inferences that would otherwise have likely been masked by the lack of statistical power induced by not treating observations as a biological process time series and the variance associated with the observation process (Paterson et al. 2019b). Detecting the effects of carnivore harvest on ungulate populations is difficult (e.g., National Research Council 1997, Hurley et al. 2011), and our approach, which accounted for the process and observations separately, allowed for stronger inference regarding these relationships. Future work should investigate the degree to which sampling design influences observation error, and the relative impact of the ratio of process variance to observation error on detecting variation in underlying biological processes (Ahrestani et al. 2013). The lack of evidence for density dependence in *per capita* recruitment rates in this study likely reflects the short duration of the time series of population data (Lebreton and Gimenez 2013), or the limitation or regulation below density-dependence thresholds by predation itself (Messier 1994). Future work with longer time series is needed to assess the evidence for density-dependent processes given the multiple potential forms for density dependence, especially given the multitude of potential factors limiting populations of wild animals including predation

(Yoccoz and Gaillard 2006, Coulson et al. 2008, Bergman et al. 2015). Additionally, the modeling approach allowed for the evaluation of the effects of mountain lion harvest management on calf recruitment in 2 ways: 1) when including the variation in other important covariates during the years of this study, and 2) by holding the other covariates constant at their median values within each area to assess only the effects of carnivore harvest management. The process variation associated with other important covariates affecting calf recruitment could mask the carnivore (or carnivore harvest) effects in certain areas or time periods, yet our population modeling methodology accounted for other covariate effects to evaluate the effect of carnivore harvest during the period it was implemented. The ability to disentangle the effects of annual variability in covariates affecting calf recruitment and the effects of the harvest treatment provides an important methodological advancement towards better understanding carnivore-ungulate population dynamics.

MANAGEMENT IMPLICATIONS

Our study demonstrates that mountain lion harvest can be an effective tool for increasing elk populations. In west-central Montana, a 2-year mountain lion harvest treatment with a prescribed 17.6% and 12.6% harvest rate resulted in a 29% reduction in mountain lion population abundance 4 years following the treatment. This reduction in the mountain lion population corresponded to increases in elk calf recruitment and population growth, although the increases in recruitment and population growth were short-term and diminished to pre-treatment levels 5 years after the harvest treatment. We caution against the generalization that these carnivore harvest rates will correspond to these specific changes in ungulate vital rates in other systems because the complex predator-prey relationships will undoubtedly vary with different carnivore assemblages, prey communities, and primary productivity.

Although our results demonstrate that carnivore harvest can be used as a tool for affecting ungulate populations, the social acceptance of regulations may challenge the implementation of these management programs. In Montana, a rural state with strongly utilitarian values, implementation of carnivore management generated social controversy, and the potential to implement such integrated carnivore-ungulate management in other states with lower percentages of residents with utilitarian-oriented wildlife values may be even less. A second challenge to the implementation of these management programs is that not all prescribed carnivore harvest quotas will be achieved using recreational hunting. In our case, strong participation in mountain lion hunting in accessible areas resulted in high management success. However, in other states and areas, hunter participation and management success may vary. Therefore, to effectively use carnivore harvest as a management tool for increasing ungulate populations, it may be more acceptable and feasible to consider lower carnivore harvest rates applied over a longer time period to achieve a more sustained and socially acceptable harvest and a slower, more sustained ungulate population response.

We recommend intensive pre-treatment and post-treatment monitoring of carnivore and ungulate populations to 1) improve understanding of the effects of carnivore harvest management as a tool for increasing ungulate populations across different

ecological systems, 2) provide reference carnivore harvest rate targets for wildlife managers prescribing carnivore harvest to achieve specific ungulate population responses, and 3) quantify the effectiveness (or lack of effectiveness) of integrated carnivore-ungulate management so that decision-makers can use science to inform these controversial harvest management decisions. The analytic tools for monitoring carnivore and ungulate populations presented here are widely applicable for evaluating effects of management treatments, and we recommend these or similar rigorous analytical tools be considered as a key component of monitoring programs designed to inform management.

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SUPPORTING INFORMATION

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

APPENDIX A: MOUNTAIN LION HARVEST

Table A1. Mountain lion harvest quotas and harvest by hunting district (HD) in the Bitterroot and Clark Fork study areas in west-central Montana, USA, during 2006–2017.

Prescription	HD	Year	Female quota	Male quota	Female harvest	Male harvest
Treatment	250	2006	0	4	0	3
Treatment	250	2007	0	4	0	4
Treatment	250	2008	0	4	0	1
Treatment	250	2009	1	10 ^a	0	3
Treatment	250	2010	2	15 ^a	1	3
Treatment	250	2011	3	20 ^a	3	4
Treatment	250	2012	7	7	9	5
Treatment	250	2013	6	4	4	6
Treatment	250	2014	3	5	1	3
Treatment	250	2015	3	5	2	5
Treatment	250	2016	3	5	2	2
Treatment	250	2017	3	5	2	5
Treatment	250	2018	3	5	3	3
Treatment	270	2006	0	3	0	5
Treatment	270	2007	0	3	0	2
Treatment	270	2008	0	3	0	1
Treatment	270	2009	1	10 ^a	1	4
Treatment	270	2010	2	15 ^a	1	8
Treatment	270	2011	3	20 ^a	3	6
Treatment	270	2012	7	7	6	7
Treatment	270	2013	6	4	7	4
Treatment	270	2014	4	5	5	5
Treatment	270	2015	5	6	1	6
Treatment	270	2016	5	6	6	5
Treatment	270	2017	5	6	5	6
Treatment	270	2018	5	6	7	5
Control	210	2006	0	2	0	2
Control	210	2007	0	2	0	2
Control	210	2008	0	2	0	1
Control	210	2009	0	2	0	2
Control	210	2010	2	4 ^a	0	2
Control	210	2011	2	4 ^a	1	1
Control	210	2012	0	7	0	2
Control	210	2013	0	3	0	4
Control	210	2014	1	3	1	2
Control	210	2015	1	3	1	3
Control	210	2016	1	3	0	3
Control	210	2017	1	3	0	3
Control	210	2018	1	3	1	3
Control	211/216	2006	0	2	0	0
Control	211/216	2007	0	2	0	2
Control	211/216	2008	0	2	0	2
Control	211/216	2009	0	2	0	2
Control	211/216	2010	4	10 ^a	2	4

(Continued)

Table A1. (Continued)

Prescription	HD	Year	Female quota	Male quota	Female harvest	Male harvest
Control	211/216	2011	4	10 ^a	1	4
Control	211/216	2012	2	5	2	3
Control	211/216	2013	3	5	2	2
Control	211/216	2014	3	5	1	2
Control	211/216	2015	3	5	2	3
Control	211/216	2016	3	5	2	3
Control	211/216	2017	3	5	0	2
Control	211/216	2018	3	5	0	6
Control	212/215/217	2006	0	4	0	2
Control	212/215/217	2007	0	2	0	1
Control	212/215/217	2008	0	2	0	0
Control	212/215/217	2009	0	2	0	1
Control	212/215/217	2010	1	4 ^a	0	2
Control	212/215/217	2011	1	4 ^a	0	2
Control	212/215/217	2012	0	6	0	6
Control	212/215/217	2013	0	6	0	6
Control	212/215/217	2014	1	6	1	7
Control	212/215/217	2015	1	6	1	6
Control	212/215/217	2016	1	6	2	2
Control	212/215/217	2017	1	6	1	6
Control	212/215/217	2018	1	6	1	6
Control	213/214	2006	0	1	0	0
Control	213/214	2007	0	1	0	0
Control	213/214	2008	0	1	0	0
Control	213/214	2009	0	1	0	1
Control	213/214	2010	1	2 ^a	0	0
Control	213/214	2011	1	2 ^a	0	2
Control	213/214	2012	1	2	1	2
Control	213/214	2013	1	2	1	2
Control	213/214	2014	1	2	1	2
Control	213/214	2015	0	2	0	3
Control	213/214	2016	0	2	0	2
Control	213/214	2017	0	2	0	2
Control	213/214	2018	0	2	0	1

^a In some years, there was no male subquota, only a female subquota and total harvest quota. The value displayed represents the total harvest quota.