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Coyote removal: can the short-term application of a controversial management tool improve female greater sage-grouse survival or nest success?

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Greater sage-grouse *Centrocercus urophasianus* have declined across western North America, intensifying the need for ecological research that enhances management and conservation goals. Predator–prey interactions can have widespread ecological effects but there is a paucity of information about predator effects on sage-grouse ecology. During a two-year study from 2011–2012, we modified the existing framework designed for predator management to test the effects of coyote *Canis latrans* removal on female sage-grouse survival and nest success in the Bighorn Basin of Wyoming, USA, where coyotes were found to be the dominant predator. We used VHF radio-telemetry to monitor female survival and locate nests over pre-treatment and treatment breeding seasons, and for one-year post-treatment to the next breeding season. During treatment, we manipulated predator management at three sites to have targeted, non-targeted, and no coyote removal. Female survival remained constant over the nesting period when treatment was applied, and there were little differences between one-year pre- ($\hat{S} = 0.64$, 90% CI = 0.38, 0.90) and one-year post-treatment survival estimates ($\hat{S} = 0.71$, 90% CI = 0.55, 0.87) at the targeted coyote removal site. No differences were detected in the daily survival rates of nests relative to coyote removal. We conclude removing coyotes, the primary predator of nests and adult females identified within this system, did not improve female survival or nest success. However, long-term monitoring is recommended to provide a more robust understanding of this complex relationship.

Lethal control programs targeting native predators to increase populations of game birds and mammals has a long history in the United States (Leopold 1946, Beasom 1974, Reynolds and Tapper 1996, Schroeder and Baydack 2001). However, the longevity of predator removal effects to protect bird populations has been questioned (Côté and Sutherland 1997, Smith et al. 2010, Ellis-Felege et al. 2012). Potential indirect interactions resulting from predator removal have been hypothesized to include apparent competition (Holt 1977), exploitative competition (MacArthur and Levins 1967), and mesopredator release (Mezquida et al. 2006). Côté and Sutherland (1997) found that predator removal had a large, positive effect on the hatch success and post-breeding population size of target bird species, but smaller effects on breeding population size. Despite these ambiguous results, managers seeking tangible actions often implement predator removals to enhance ground-nesting bird populations.

Greater sage-grouse *Centrocercus urophasianus* (hereafter sage-grouse) distribution and population densities have declined across western North America, and the species occupies only 56% of its historic range (Schroeder et al. 2004). The severity and extent of this decline led to sage-grouse candidacy for protection under the Endangered Species Act of 1973, but the United States Fish and Wildlife Service recently decided that listing of sage-grouse was not warranted (USFWS 2015).

Relatively low and variable reproductive rates and high annual adult survival differentiate sage-grouse from other grouse species (Connelly et al. 2011, Taylor et al. 2012). Female survival, chick survival, and nest success account for 73–75% of the variation in sage-grouse population growth rates, and most is tied to female survival (Taylor et al. 2012). The persistence of populations may rely on conservation actions that simultaneously improve multiple vital rates.

Predation has been identified as a primary factor influencing sage-grouse nest success in some systems (Lockyer et al. 2013), and excessive nest predation can result in reduced productivity (Autenrieth 1981, Gregg et al. 1994, Gregg and Crawford 2009). Several species have been documented as predators of sage-grouse (e.g. golden eagle *Aquila chrysaetos*,

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coyote, American badger *Taxidea taxus*, northern harrier *Circus cyaneus*; Boyko et al. 2004) and their nests (common raven *Corvus corax*, black-billed magpie *Pica hudsonia*, long-tailed weasel *Mustela frenata*, striped skunk *Mephitis mephitis*; Coates et al. 2008, Dahlgren 2009, Lockyer et al. 2013).

The association between disturbed and fragmented landscapes, lower breeding success commonly attributed to interactions with generalist predators, and predator community structure add complexity to understanding the causes and consequences of predation on ground-nesting birds (Kurki et al. 2000, Coates and Delehanty 2004, 2010). Predation can exacerbate or dampen oscillations in abundance, and, in extreme cases, limit prey populations to the point of extinction (Mills 2013). Efforts to improve habitat indirectly mitigate predation effects through increased concealment cover, but may provide only limited success if large-scale factors associated with predator densities are not considered (Coates and Delehanty 2004, Manzer and Hannon 2005, Dinkins et al. 2016). The need to understand and address these effects lead to predator removal actions being proposed for a sage-grouse population in the Bighorn Basin of Wyoming, USA.

The goal of our study was to identify the key predator of female sage-grouse and their nests in the Bighorn Basin system and evaluate the effect of removals targeting that predator on sage-grouse survival and nest success. Our primary research objectives were: 1) to identify which predators were affecting sage-grouse nest success and survival and 2) determine if the removal of coyotes improved female survival or nest success. Understanding the effects of predation and coyote removal will supplement information on optimizing the cost-effectiveness of sage-grouse management beyond habitat improvement.

Material and methods

Study area

From 2011 to 2012, we studied predation of female sage-grouse and nests in the northwest portion of Bighorn Basin, Wyoming, USA (Fig. 1). Bighorn Basin is a semi-arid, intermontane basin that encompasses 32 000 km² of Bighorn, Hot Springs, Park and Washakie Counties. Elevation in the Basin ranged from 1220 to 1525 m and the area was composed of badland topography, intermittent buttes, and big sagebrush *Artemisia tridentata* spp. communities. The study area included 513 km² of Bighorn Basin, and we conducted the study at three lek complexes: Oregon Basin (44°22'45"N, 108°48'17"W), 15 Mile (44°10'89"N, 108°44'38"W), and Polecat Bench (44°57'00"N, 108°45'54"W). We defined each study site as a 171-km² area with one or more active lek and surrounding nesting areas used by sage-grouse in each lek complex. Average maximum and minimum temperatures during the study period (March to September) were 25.7°C and -0.4°C, respectively in 2011 and 29.7°C and 0.1°C in 2012. Total precipitation during the study period was 14.7 cm in 2011 and 19.5 cm in 2012 (Fales Fock, WY, USA; < www.raws.dri.edu/cgi-bin/rawMAIN.pl?wyWFAL >).

Bighorn Basin was composed of mostly public land managed by the Bureau of Land Management (40%), Forest Service (25%), state (5%), or other federal agencies (>1%), and private land (25%; Sage-grouse Conservation Plan for the Bighorn Basin, WY 2007). The proportion of land uses were similar in the study sites and included livestock grazing, wildlife habitat, dry-land and irrigated crop production, recreation, bentonite mining and oil and gas extraction. Vegetation communities included shrubs (e.g. sagebrush

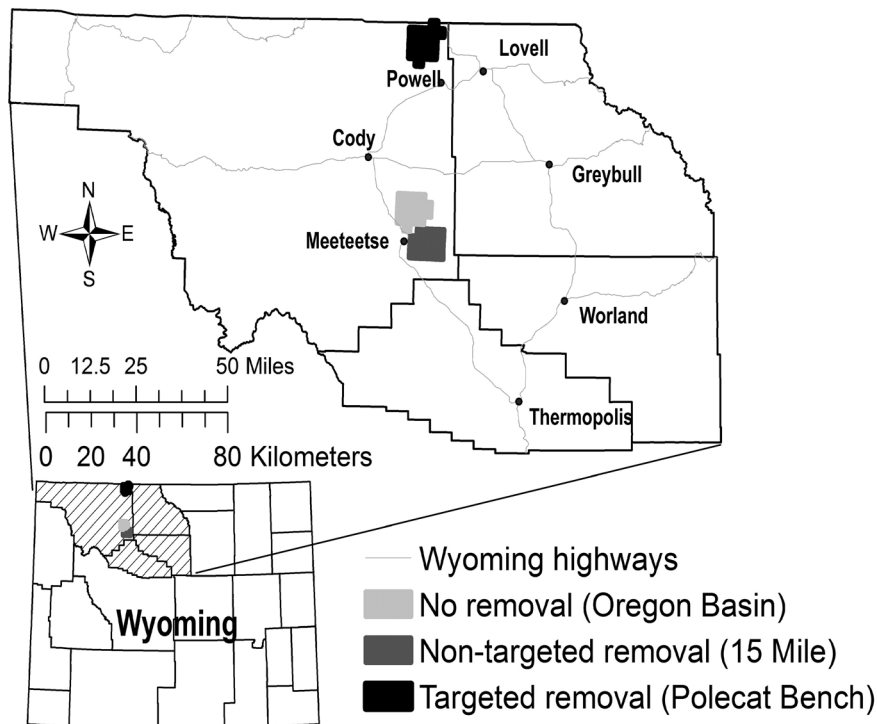


Figure 1. Location of Bighorn Basin in Wyoming, USA, and three sites experimental coyote removal was implemented to test the effects of targeted, non-targeted and no coyote removal treatments on female greater sage-grouse survival and nest success from 2011–2012.

spp., greasewood *Sarcobatus vermiculatus*, rabbitbrush *Chrysothamnus viscidiflorus*, forbs (e.g. globemallow *Sphaeralcea* spp., milkvetch *Astragalus* spp., phlox *Phlox* spp.), perennial grasses (e.g. blue-bunch wheatgrass *Pseudoroegneria spicata*, blue grama *Bouteloua gracilis*), and invasive species (e.g. cheatgrass *Bromus tectorum*, knapweed *Centaurea* spp.). Detailed descriptions of vegetative characteristics for Bighorn Basin can be found in Hess and Beck (2012a).

The composition of mammalian predators was similar among treatment sites and between years (Orning 2014). The most commonly detected mammalian predator across all three lek complexes was coyote, followed by red fox *Vulpes vulpes* (detected from scent stations, camera traps, scat transects, and nest cameras, Orning 2014). Other mammalian predators detected included bobcat *Lynx rufus*, badger, striped skunk, raccoon *Procyon lotor* and weasel *Mustela* spp. Avian predators were also similar between sites and across years and included golden eagle, northern harrier, red-tailed hawk *Buteo jamaicensis*, common raven, black-billed magpie and other Corvidae/Icteridae species (detected from point counts; Orning 2014).

Study design

In 2011, we identified predators of female sage-grouse and nests at two sites in the northwest portion of Bighorn Basin. We collected pre-treatment data (one year prior) on sage-grouse vital rates, because 1) the primary predator(s) of sage-grouse were unknown and 2) these sites differed in historic predator management strategies. Based on USDA-APHIS Wildlife Services (WS) activities (Jim Perhringer, pers. comm.), we designated Oregon Basin and Polecat Bench as sites representative of no coyote removal and coyote removals, respectively. We added a third site in 2012, called 15 Mile, to implement an experimental removal design that included three treatment levels of coyote removal (Fig. 1) to test the effects on female survival and nest success. We did not have pre-treatment data for the third site, therefore we caution direct comparison of this site to other sites but provide estimates and discussion on relative effects for that site. The study was approved by the USDA-National Wildlife Research Center's Institutional Animal Care and Use Committee (IACUC) under protocol QA-1860.

Coyote removal

Coyote removals were conducted by WS in Bighorn Basin over the course of the study. Removal methods included aerial gunning, snare and leg-hold trap, den gassing and opportunistic shooting. Coyotes were removed year-round for domestic livestock depredation and agriculture damage at Polecat Bench, the targeted removal site. We refer to this site as the targeted removal treatment because, in the second year, lethal removals exceeded normal removal management activities and were focused in sage-grouse nesting habitat from 14 March – 15 June 2012. Coyote removals at the non-targeted treatment site, 15 Mile, were conducted exclusively for mule deer *Odocoileus hemionus* fawn production. This site was included in the second (treatment) year to contrast differences between targeted and non-targeted removal efforts as it relates to sage-grouse enhancement, no

pre-treatment data existed for the site. No coyote removal occurred in Oregon Basin either year, and this site served as the experimental control for the study. Hereafter for clarity, we refer to the three study sites as targeted, non-targeted, and no removal sites.

Based on coyote behavioral ecology we believe populations of coyotes at our treatment sites were independent. Coyotes in this region have home ranges of 13.12 (\pm 1.59) km² (Berger and Gese 2007), with dispersal to adjacent packs over 40 km (Gese et al. 1996). The targeted removal site was 80 and 66 km from the non-targeted and no removal sites, respectively. The non-targeted and no removal sites were adjacent sites 16-km apart (central points), but separated by the Greybull River, limiting potential coyote range overlap between the two sites (Gese et al. 1996).

Female sage-grouse monitoring

From March to April of both years, we captured female sage-grouse under Wyoming Game and Fish Department Chapter 33 permit ID no. 802 on two leks at each site using rocket nets (Giesen et al. 1982). Females were fitted with VHF necklace style transmitters (Advanced Telemetry Systems Inc. [ATS]) and were classified as yearling (first breeding season) or adult (\geq second breeding season) based on wing primary morphology (Eng 1955, Dalke et al. 1963). Transmitters weighed 22 g and had a battery life expectancy of 869 days. We monitored survival using VHF every 48–72 h from the time of capture through the end of the brood-rearing season (August). Female mortalities were investigated by WS personnel within 72 h of signal detection to determine cause-specific mortality when possible. Several sources of forensic evidence were used to determine cause of death including carcass age (decay, exposure to sun/elements) and condition, time since last live signal detection or visual proof of life (or kill events) from trail cameras placed on nests, feeding patterns and hemorrhaging (bite spread), collar retrieval locations (dens, buttes, perches), and tracks, signs of struggle, blood or other evidence at attack scenes (Redpath et al. 1998, Beck et al. 2006).

Nest monitoring

We located nests after obtaining three consecutive locations of a radio-collared female in the same 10–20 m area (Holloran and Anderson 2005). Nests were all located in either the laying period or initial stages of incubation. We then placed infrared Bushnell Trophy Cam trail cameras (Bushnell Outdoor Products) 3–5 m from the nest's entrance or exit. Cameras were mounted on 1-m rebar stakes on average 41 cm above ground and were concealed using sagebrush to camouflage and prevent use as a perch. We wore rubber boots to minimize human scent and did not approach nests if avian predators were visible when cameras were initially set or to replace batteries and memory cards.

We continued to monitor female sage-grouse via telemetry to confirm their location on nests from a distance \geq 50 m and obtained visual confirmation when camera memory cards were changed every seven days. Cameras were used until nests hatched or failed. All nests were categorized as successful (\geq 1 egg hatched) or unsuccessful (Rearden

1951) as determined by eggshell cap and shell membrane condition (Wallestad and Pyrah 1974). Hatch dates were determined by nest camera evidence, telemetry (day mid-way between consecutive locations), or calculated based on an average incubation time of 27 days from nest initiation (Schroeder et al. 1999). Nest camera photographic evidence was the primary method used to identify nest predator species, supported by secondary field evidence from predator tracks, and scat. We also used DNA analysis on a sample of depredated egg remains in 2012 to enhance evidence from nest cameras (Hopken et al. 2016).

Statistical analysis

We used Cox proportional hazard models in program R to analyse covariates and produce survival estimates of female sage-grouse (< www.r.project.org >, Fox 2002). To estimate the effect of coyote removal on female survival, we adjusted for other possible explanatory variables by including age, season, and year covariates in our a priori model set. We also added a covariate for whether a bird was nesting (1 = nesting, 0 = not nesting) at time of death. We evaluated female survival for coyote removal treatment effects over: 1) one-year pre-treatment (1 April 2011 – 29 Feb 2012), 2) the nesting period when treatment was applied (1 March 2012 – 15 June 2012), 2) six-months post treatment (1 March 2012 – 31 August 2012), and 3) one-year post treatment (1 March 2012 – 1 March 2013). We report survival estimates (\hat{S}), hazard ratios (HR) and associated 90% confidence intervals for model covariates with evidence supporting the importance of effect as described below.

Nest models (Dinsmore et al. 2002) were analysed in Program MARK (ver. 6.1, White and Burnham 1999) to estimate daily survival rates (DSR). We developed a set of candidate models to examine covariate effects of treatment site (g), bird age (Age), age of nest (Nest age), and time on nest survival. We investigated within year temporal effects by testing for differences in nest survival based on constant (.), linear (T), log-linear (lnT), and quadratic (TT) time trends. We tested for these temporal effects because we believed they would account for temporal and environmental variation in detection by predators over the duration of nesting (laying/incubation). We report nest success as a function of the DSR using

$$\widehat{NS} = DSR^{37}$$

where 37 is the time required in days for a nest to hatch including nest initiation and incubation (37 days; Coates and Delehanty 2010). To account for parameters that are a function of other parameters (NS as a function of DSR), we followed methods described in Powell (2007) to calculate variances and confidence intervals for nest success using the delta method (Seber 1982).

We used Akaike's information criterion (Akaike 1973) corrected for small sample sizes (AIC_c) to evaluate model fit (Burnham and Anderson 2010). We also evaluated covariate effects based on regression coefficients (β) and their associated 90% confidence intervals for overlap of 0 as a measure of the strength of evidence for variable effects (Anthony et al. 2006, Forsman et al. 2011). We considered covariates from competitive models with < 10% of CI overlapping 0 ('slightly'

overlapping) to have less evidence of effect compared with covariates with no interval overlap of 0, and covariates with > 10% of confidence limits above or below 0 to be 'widely' overlapping and to have no support for importance of effect (Dugger et al. 2016). Because our primary goal in this analysis was to evaluate the effect of coyote removal (treatment) on vital rates, when appropriate we used the best model that included an effect of coyote removal to produce female and nest survival estimates.

Results

We captured 25 females (n = 10 targeted; n = 15 no removal) from four leks in Bighorn Basin in spring 2011 (Table 1). Eleven females survived over winter and 44 additional females were captured and radio collared from three lek complexes for the second year of the study in 2012 (Table 1).

Wildlife Services removed 118 coyotes from the two treatment sites over the study (Table 1). During the coyote removal treatment period (nesting) in 2012, 9 and 18 coyotes were removed from the non-targeted and targeted removal sites, respectively. Wildlife Services removed an additional 45 coyotes from the targeted removal site by the end of the nest/brood monitoring period in 2012, representing a 37% increase over pre-treatment year.

Pre-treatment female survival

Twelve of 25 females died (48%) during the first year of the study, nine of which were in no removal site and three in the targeted removal site. Coyotes were the most identified predators of sage-grouse females with other deaths attributed to badgers, golden eagles, and unknown cause of death (Supplementary material Appendix 1 Table A1.1). Female mortality was detected on average 2.8 days (range: 1–5 days) after predation for all females monitored weekly. We censored three females from survival analysis in 2011 (emigration, capture myopathy, slipped radio collar). We only considered univariate covariate effects over the pre-treatment year and did not observe evidence that bird age ($\beta = 0.09$, SE = 0.61, 90% CI = -0.91 to 1.09) or site ($\beta = -0.835$, SE = 0.67, 90% CI = -1.94 to 0.27) influenced survival.

Table 1. Sample sizes of female sage-grouse radio-collared, nest, mortality and removed coyote at two lek complexes observed for pre-treatment (2011) and three lek complexes treated with variable levels of coyote removal in Bighorn Basin, Wyoming, USA (27 March – 31 August 2012).

| Year | No removal | | Non-targeted removal | | Targeted removal | |
|------------------------------|------------|-----------------|----------------------|-----------------|------------------|-----------------|
| | 2011 | 2012 | 2011 | 2012 | 2011 | 2012 |
| Radio collars | 15 | 19 ^a | – | 16 | 10 | 20 ^b |
| Coyotes removed ^c | 0 | 4 ^d | – | 9 | 46 | 63 ^e |
| Nests | 15 | 10 | – | 10 ^f | 9 | 15 ^f |
| Mortalities | 9 | 7 | – | 6 | 3 | 5 |

^aIncludes 5 females that survived from 2011.

^bIncludes 6 females that survived from 2011.

^cNo. coyotes removed over annual period (included dependent pups).

^dRoad killed, all < six months old.

^eNo. coyotes removed over six-month period (included dependent pups).

^fIncludes second nest attempts.

Post-treatment female survival

Eleven females died during the 2012 coyote removal treatment period and seven more died by the end of the study (1 Mar 2013). Raptors (golden eagle and unknown spp.) were the most identified predators of females post-treatment, with other deaths attributed to coyote, unknown canid spp., human-caused, and unknown cause of death (Supplementary material Appendix 1 Table A1.1). Three females were censored from analysis in 2012 (two left study area, one was never detected). Mortality was detected on average 3.5 days (range: 0–8 days) after mortality event for all females monitored weekly.

During the nesting period, the best approximating model indicated constant survival of females across sites (Table 2). The second model indicated an age effect on survival, but the coefficient confidence intervals overlapped widely ($\beta=0.83$, 90% CI = -0.31 to 1.97), and we excluded it from consideration. The treatment model did not rank among competitive models but there was evidence of a large negative effect ($\beta=-1.22$, 90% CI = 0.17 to 2.27; HR = 0.30, 90% CI = 0.10 to 0.85).

The top model for the six-month post-treatment period included an effect for nesting status ($\beta=2.92$, 90% CI = 1.92 to 3.92; HR = 18.54, 90% CI = 6.80 to 50.57). The second model included a treatment effect (site), but was not competitive ($\Delta AIC_c > 5$, Table 2), and had no support for evidence ($\beta=-0.74$, 90% CI = -1.57 to 0.99).

Similar to the nesting period, the best approximating model one-year post-treatment period indicated constant

Table 2. Model selection results based on Cox proportional hazard regression for sage-grouse survival at three sites treated with coyote removal in Bighorn Basin, Wyoming, USA (2012). Models are ranked according to Akaike's information criterion corrected for small sample sizes (AIC_c).

| Model ^a | K^b | AIC_c | ΔAIC_c | w_i^c |
|--------------------|-------|---------|----------------|---------|
| Removal treatment | | | | |
| Null | 1 | 78.832 | 0.000 | 0.480 |
| Age | 2 | 79.410 | 0.577 | 0.360 |
| Site | 4 | 81.916 | 3.084 | 0.103 |
| Site+Age | 5 | 83.101 | 4.268 | 0.057 |
| Six-month post | | | | |
| Nesting | 2 | 98.282 | 0.000 | 0.945 |
| Site+ Nesting | 5 | 103.992 | 5.710 | 0.054 |
| Age | 2 | 113.944 | 15.662 | 0.000 |
| Null | 1 | 115.461 | 17.179 | 0.000 |
| Site+Age | 5 | 119.498 | 21.216 | 0.000 |
| Site | 4 | 120.188 | 21.906 | 0.000 |
| One-year post | | | | |
| Null | 1 | 243.392 | 0.000 | 0.206 |
| Year | 2 | 243.764 | 0.372 | 0.171 |
| Age+Year | 3 | 243.904 | 0.512 | 0.159 |
| Site | 3 | 244.113 | 0.721 | 0.143 |
| Age | 2 | 244.400 | 1.008 | 0.124 |
| Site+Age | 4 | 245.546 | 2.153 | 0.070 |
| Site+Year | 4 | 245.753 | 2.361 | 0.063 |
| Site+Age+Year | 5 | 246.518 | 3.126 | 0.043 |
| Site × Year | 5 | 248.062 | 4.670 | 0.020 |

^aSite refers to level of coyote removal effort (targeted, non-targeted, no); Age refers to if a hen was a juvenile or an adult; Nesting refers to if a female was nesting or not; Year refers to baseline or treatment year of study; and Null is constant survival.

^bNo. of parameters in model.

^cAkaike weight.

survival. However, four models were considered competitive (Table 2). The second model indicated a negative but unmeasurable influence of year on survival ($\beta=-0.49$, 90% CI = -1.16 to 0.18). Age appeared in two of the four top models, but importance of effects were unsupported ($\beta=0.49$, 90% CI = -0.14 to 1.12). There was evidence for support of an effect based on treatment (site) with coefficient confidence intervals slightly overlapping 0 ($\beta=-0.53$, 90% CI = -1.20 to 0.14; HR = 0.59, 90% CI = 0.30 to 1.16). Because of model selection uncertainty, and evidence there was support for a treatment effect, we used the site model for interpretation of treatment effects over the annual period to compare with one-year pre-treatment estimates (Table 3).

Estimates of female survival remained fairly constant (1.11 times higher) between pre- and post-treatment years at the targeted removal site, while female survival was 1.44 times higher between years at the no removal site (Table 3). The lack of improvement in female survival in the targeted removal site from pre-treatment, where 46 coyotes were removed over 12 months (3.8 coyotes month⁻¹), to post-treatment, over which 63 coyotes were removed in six months (10.5 coyotes month⁻¹) suggest the limited nature of survival gains relative to coyote removal. However, confidence intervals suggested there were no measurable differences in survival between sites or among years.

Pre-treatment nest survival

We documented 24 nests from 22 females between 28 April and 16 June 2011. The second nests were in the no removal site. We set trail cameras on 21 (three failed prior to cameras) of 24 nests and documented 11 complete nest predation events and two partial nest predation events.

The most common nest predators identified were coyote, followed by raven and bobcat (Supplementary material Appendix 1 Table A1.2). For all nests (successful and unsuccessful), individual area nest predation was 67% ($n=6$) and 47% ($n=7$) in the pre-treatment targeted and no removal sites. Of unsuccessful nests, nest failures due to abandonment or female mortalities were 30% and 14% in the pre-treatment targeted and no removal sites, respectively.

No differences were observed in the DSR rates of nests between the targeted and no removal sites in 2011

Table 3. Female greater sage-grouse survival estimates (\hat{S}) from Cox regression model one-year pre-treatment (1 Apr 2011 – 30 March 2012) and one-year post-treatment (1 Apr 2012 – 1 March 2013) at three sites treated with coyote removal in the Bighorn Basin, Wyoming, USA, 2011 – 2012.

| Time period | \hat{S} (SE) | 90% CI |
|-----------------------------|----------------|------------|
| One-year pre | | |
| No treatment | 0.36 (0.13) | 0.15, 0.57 |
| Coyote removal ^a | 0.64 (0.16) | 0.38, 0.90 |
| One-year post | | |
| No treatment | 0.52 (0.11) | 0.34, 0.70 |
| Non-targeted treatment | 0.66 (0.12) | 0.46, 0.86 |
| Targeted treatment | 0.71 (0.10) | 0.55, 0.87 |
| Coyote removal ^b | 0.69 (0.10) | 0.53, 0.85 |

^aCoyote removal site in 1st year is site that received targeted coyote removal treatment in 2nd year.

^bNon-targeted and targeted coyote removal treatment levels combined.

(Supplementary material Appendix 1 Table A1.3 and A1.4 for AIC_c and beta estimates). Constant survival yielded a 37-day nest success estimate of 32.9% (90% CI = 11.6% to 54.2%).

Post-treatment nest survival

We documented 34 nests (two renests) from 32 nesting females from 13 April to 18 May 2012 across the three treatment sites in Bighorn Basin. We set trail cameras on 34 nests ($n_{No} = 10$, $n_{Non-targeted} = 10$, $n_{Targeted} = 14$) and observed 15 nest predation events. Most common nest predators identified post-treatment in order of frequency was coyote, raven, skunk and red fox (Supplementary material Appendix 1 Table A1.2). Cameras successfully identified depredating species for nine nest predation events; lab forensics additionally identified species for two predation events not captured by cameras and confirmed photo evidence for four camera-documented predations (Hopken et al. 2016). Trail cameras and lab forensics failed to identify depredating species for three nests at the targeted removal site.

The best nest model indicated constant DSR of nests across treatment sites. All six models that were considered competitive ($\Delta AIC_c < 2$) had confidence intervals that overlapped 0 and little to no support for effects on nest survival (Table 4). The site (treatment) model suggested a negative consequence to DSR with increased coyote removal effort, with lower estimates in the targeted removal site than the no removal site. However, there was no support for the effect ($\beta = -0.56$, 90% CI = $-1.58, 0.45$). Constant survival during treatment yielded a 37-day nest success estimate of 39.1% (90% CI = 22.9% to 55.2%).

Discussion

Our study begins to examine the question of predator effects on sage-grouse ecology and provides a baseline to examine the effects of predator removal and predation in other sage-grouse systems. The decline of sage-grouse

Table 4. Model selection results for daily survival rate (DSR) of sage-grouse nests at three sites treated with coyote removal in Bighorn Basin, Wyoming, USA (2012). Models are ranked according to Akaike's information criterion corrected for small sample sizes (AIC_c).

| Model ^a | K^b | AIC_c | ΔAIC_c | w_i^c |
|--------------------------------------|-------|---------|----------------|---------|
| S(.) | 1 | 113.923 | 0.000 | 0.206 |
| S(Nest age + Nest age ²) | 3 | 114.608 | 0.685 | 0.146 |
| S(lnT) | 2 | 114.667 | 0.744 | 0.142 |
| S(g) | 3 | 114.883 | 0.960 | 0.128 |
| S(Nest age) | 2 | 115.511 | 1.589 | 0.093 |
| S(T) | 2 | 115.587 | 1.665 | 0.090 |
| S(T + TT) | 4 | 115.943 | 2.021 | 0.075 |
| S(g + lnT) | 4 | 116.247 | 2.324 | 0.064 |
| S(TT) | 3 | 117.920 | 3.997 | 0.028 |
| S(g + T + TT) | 5 | 117.941 | 4.018 | 0.028 |

^a(g) refers to the treatment group based on the level of coyote removal (targeted, non-targeted, no); T is a linear time trend; TT is a quadratic time trend; Nest age refers to age of nest and is based on nest initiation date; and (.) is constant survival.

^bNo. of parameters in model.

^cAkaike weight.

invariably includes a multitude of complex interactions between habitat, predator density, and anthropogenic factors (Crawford et al. 2004, Moss et al. 2010, Hess and Beck 2012b, Dinkins et al. 2014b, Howe et al. 2014). We examined predation and coyote removal effects in a central, non-fringe sage-grouse population, constraining the application of information based on our results to populations with similar limiting factors. For example, predator removal may have different effects in areas where mortality from predators is greater. The question of whether predation is an exacerbating secondary factor will be population specific, and predation may vary spatially and temporally within a given population. Nevertheless, identifying the role predation plays in a specific population's system is imperative to test and understand in order to provide the most effective management.

We identified coyotes as the species most responsible for both nest predation events and female mortalities in 2011. Then in 2012, we applied coyote removal as a treatment during the nesting period, and survival of females was unaffected during the course of treatment through 6-months post-treatment. Further, we did not detect a one-year lag in effects, as pre- and post-treatment annual survival at the targeted removal site were relatively constant. Environmental conditions can result in variable monthly or seasonal survival while maintaining stable annual survival patterns for female sage-grouse (Blomberg et al. 2013b). Our understanding of the biotic and abiotic factors influencing this vital rate is just beginning to emerge (Gutery et al. 2013), and sage-grouse show large annual fluctuations in vital rates across their range (Crawford et al. 2004, Taylor et al. 2012). We had small sample sizes and a short study duration, therefore, even though we used an experimental approach, it is unclear what effect natural variation had on our estimates. There were no measurable differences in sage-grouse nest survival in response to experimental removal of coyotes. The differences in 2011 site-specific estimates of DSR were small. In addition, DSR extrapolated nest success estimates were already different between sites in 2011, 18% higher in the no removal site, affecting the magnitude of change possible and our ability to detect a response. Similarly, Dinkins et al. (2016) documented that lower sage-grouse nest success was associated with an interaction between lethal coyote removal and precipitation, which they attributed as indicative of mesopredator release. Subsequent years of nest monitoring for our study sites produced similar site-specific estimates of nest success (Taylor et al. 2017), suggesting that while long-term monitoring is more capable of accounting for annual variation, short-term research, like our study, can produce meaningful results consistent with multi-year studies.

As a field experiment, we designed our treatment levels to augment existing management removal efforts. Accounted for as effort in this study, we believe the increased number of coyotes removed between years in the targeted removal site provided an accurate assessment of coyote removal effects on survival and nest success. The number of coyotes removed and the response we observed were relative to coyote population densities at those sites, such that targeted and non-targeted removal efforts might not have resulted in lower density coyote populations.

Between the two years of the study, we observed a shift from coyote-dominated nest predation events to equal numbers of coyote and raven nest predation events. Similarly, there was a shift in the primary predator of females from coyotes to raptors, despite consistent raptor abundance between years (Orning 2014). Inter-guild compensatory shifts in nest predators was observed in response to predator removal for northern bobwhite *Colinus virginianus* (Ellis-Felege et al. 2012). Such a shift establishes the potential for similar relationships in our system, and suggests a potential indirect effect. Consistent with emerging evidence that survival is influenced primarily by climatic factors, our results suggest that predation is not likely the principal driver of female sage-grouse survival in Bighorn Basin (Blomberg et al. 2013a, b, Guttery et al. 2013, Dinkins et al. 2014a). We consider the lack of improvement in females surviving at the targeted removal site as further support predation was secondarily exacerbating to sage-grouse mortality.

Solutions to address declining sage-grouse numbers must consider the multitude of influential factors affecting sage-grouse ecology (livestock grazing, fire regime, disease, predation and oil and gas development). Our results suggest short-term prescribed coyote removal during the nesting period did not improve female survival or nest success. Determining if lagged fitness effects from predator removal exist that could translate into higher growth rates or long term population benefits will require sustained efforts. Compensatory shifts in predators, natural annual variation, or predator density factors may be causing the observed results in Bighorn Basin. Conducting experimental predator removals over multiple years and with larger sample sizes should improve detection of observable patterns (cycles, density-dependence, etc.). Beyond retrospective evaluation, we conducted a field quasi-experiment to quantify predation effects through targeted predator manipulation. Our research begins to provide information quantifying the influence of predators on two important sage-grouse vital rates (female survival and nest success) and we implemented a framework for monitoring changes in sage-grouse populations that could enhance management decisions in Bighorn Basin.

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Supplementary material (available online as Appendix wlb-00345 at <www.wildlifebiology.org/appendix/wlb-00345>). Appendix 1.