

# Effects of common raven and coyote removal and temporal variation in climate on greater sage-grouse nesting success



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## ABSTRACT

Predator removal has been simultaneously proposed and criticized as a mitigation measure for low reproductive rates of prey species, including greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse"). Depredation of sage-grouse nests can limit their productivity. In Wyoming, lethal removal of common ravens (*Corvus corax*; hereafter "ravens") and coyotes (*Canis latrans*) has been conducted by USDA/APHIS/Wildlife Services (WS) for the protection of livestock. During 2008–2011, we evaluated sage-grouse nest success in study sites (1) where WS initiated a raven removal program, (2) WS removed coyotes, and (3) WS did not manipulate ravens and/or coyotes. Precipitation and temperature were analyzed individually and as interactive effects with coyote removal numbers as sources of annual variation in nest success. Over the course of our study, raven densities decreased at study sites with WS raven removal, while sage-grouse nest success in those study sites was higher during years with reduced raven density. Temperature effects on nest success were dependent on timing with successful nests having cooler temperatures prior to the nesting season (conditions promoting water retention and grass growth) and warmer temperatures the week before nest fate (conducive to degradation of sage-grouse odorants used by mammalian predators). Lower nest success was associated with more lethally removed coyotes interacting with greater precipitation suggesting mesopredator release. Raven removal may have a place in sage-grouse management as an interim mitigation measure when sage-grouse populations are subjected to high densities of ravens. However, long-term solutions are necessary, such as reducing supplemental food sources and perch structures used by ravens.

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## 1. Introduction

Predator removal has been employed worldwide as a mechanism to increase reproductive rates of upland game species. Unlike other population limiting factors (e.g., habitat, weather, and drought), predation may be reduced by wildlife management agencies (Cote and Sutherland 1997). For example, removal of red fox (*Vulpes vulpes*), carrion crow (*Corvus corone*), and mustelids led to increases in breeding populations of lapwing (*Vanellus vanellus*), golden plover (*Pluvialis apricaria*), and red grouse in northern England (*Lagopus lagopus scoticus*; Fletcher et al., 2010). However, predator removal has been connected with increased reproductive success without increase in bird population size for black grouse (*Lyrurus tetrix*) and willow ptarmigan (*Lagopus*

*lagopus*; Parker, 1984) and sandhill cranes (*Grus canadensis*) and Eurasian curlews (*Numenius arquata*; Madden et al., 2015).

Greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") abundance in western North America has declined over the last century (Connelly et al., 2011, Garton et al., 2011, Nielson et al., 2015). Many factors have been attributed to this decline including habitat loss, habitat fragmentation, habitat degradation, and predation (Connelly et al., 2011, USFWS, 2015). However, there are no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult), and Hagen (2011) suggested that in general predation is not limiting sage-grouse population growth. Concurrently, common raven (*Corvus corax*; hereafter "ravens") abundance has increased throughout the historic range of sage-grouse following human development (Andrén, 1992, Boarman et al., 1995, Engel and Young, 1992, Larsen and Dietrich, 1970, Sauer et al., 2011). Raven depredation of sage-grouse nests has been implicated as a potential factor limiting sage-grouse productivity especially in fragmented habitats (Batterson and Morse, 1948, Bui et al., 2010, Coates and Delehanty, 2010, Gregg et al., 1994, Lockyer et al., 2013, Schroeder and Baydack, 2001, Willis et al., 1993). Thus, raven removal may serve to provide a release of nest

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depredation rates in fragmented habitats and areas with human-subsidized raven populations.

Similar to ravens, coyote abundance has been suggested as a limiting factor to sage-grouse productivity (Batterson and Morse, 1948, Willis et al., 1993). Lower sage-grouse productivity after the early-1970s has been anecdotally connected to increased abundance of coyotes throughout the western United States after the 1972 banning of wide spread application of the poison 1080 on federal lands (Executive Order 11,643 and EPA PR Notice 72-2; Heath et al., 1997, Willis et al., 1993). Coyote depredation of sage-grouse nests has been documented with videography and genetic analyses (Lockyer et al., 2013, Orning, 2013). However, coyote abundance has not been associated with unusual depredation rates of sage-grouse nests (Orning, 2013, Slater, 2003).

Lethal removal of coyotes has been associated with changes in predator community abundances and behavior with smaller mammalian predators increasing in abundance and distribution (mesopredator release; Crooks and Soulé, 1999; Prugh et al., 2009). Mesopredator release has been associated with increased negative effects of secondary mammalian predators (e.g., red fox, raccoon [*Procyon lotor*], and striped skunk [*Mephitis mephitis*]) on waterfowl nest success (Greenwood et al., 1995, Mezquida et al., 2006, Prugh et al., 2009, Sovada et al., 1995). Mezquida et al. (2006) suggested that lethal removal of coyotes may induce indirect negative effects on sage-grouse populations, such as mesopredator release, with potential increased depredation of sage-grouse nests by badgers (*Taxidea taxus*), red foxes, and ravens.

In response to raven depredation of livestock, lethal removal of ravens (hereafter “raven removal”) was initiated by WS in Carbon, Lincoln, Sweetwater, and Uinta counties in Wyoming, 2007–2011. This provided a unique opportunity to study the potential effects of raven removal on sage-grouse nest success. Thus, we evaluated the change in density of ravens and sage-grouse nest success in areas associated with WS raven removal efforts and areas farther away during 2008–2011. While the focus of our study was to assess the effect of WS removal of ravens on sage-grouse nest success, WS also manipulates coyote populations annually via lethal removal for the benefit of livestock and in some cases wildlife. Thus, we evaluated nest success of sage-grouse in study sites (1) where WS initiated a raven removal program, (2) WS lowered the abundance of coyotes, and (3) WS did not manipulate ravens and/or coyotes.

The foraging ability of olfactory predators should be enhanced by cool wet conditions and reduced by hot dry conditions (Conover, 2007, Gutzwiller, 1990, Ruzicka and Conover, 2012). However, precipitation also increases grass and herbaceous cover, which provide concealment and higher success to sage-grouse nests (Doherty et al., 2014, Holloran et al., 2005). As such, precipitation and temperature effects on nest success of sage-grouse may be contradictory depending on the timing of weather events. As secondary objectives, we conducted post-hoc analyses to evaluate annual variation in nest success of sage-grouse attributed to precipitation and temperature prior to the nesting season, 1-year lags, and the week before nest fate. We also considered interactive effects between precipitation and temperature and coyote removal numbers. We hypothesized that weather conditions promoting grass growth prior to the nesting season would be associated with higher sage-grouse nest success; whereas, interactive effects between weather variables and coyote removal numbers would align lower sage-grouse nest success with weather conditions conducive to predators using olfaction to locate prey.

## 2. Materials and methods

### 2.1. Study area

Our study was conducted in southwest and south-central Wyoming to evaluate the response of sage-grouse nest success to raven removal. Eight 16-km diameter study sites were located in southwest Wyoming

and approximately centered around leks where hens were captured (Fig. 1); the size of these study sites was based on results found by Holloran and Anderson (2005). In addition, four 24-km diameter study sites were located in south-central Wyoming, because sage-grouse were captured at several nearby leks over a larger area. Five out of 12 study sites were within 15 km of WS raven removal activities (Fig. 1). Study sites within 15 km of WS raven removal were considered ‘removal study sites’ and those at a distance >15 km were considered ‘non-removal study sites’. We adapted the criteria of 15 km (15-km radius equivalent to 706.5 km<sup>2</sup>) to define study sites potentially impacted by WS raven removal from reported average home-range sizes of breeding and non-breeding ravens (California 0.3–45.8 km<sup>2</sup> [Linz et al., 1992], Minnesota 27.3–195 km<sup>2</sup> [Bruggers, 1988]) and average daily movements (Mojave Desert 4.5 km [Boarman et al., 1995], Idaho 6.9 km [>95% of movements within 12.5 km; Engel and Young, 1992]). Lethal removal of coyotes was conducted by WS in all of the raven removal study sites and 5 of the 7 non-raven-removal study sites. Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming with a variety of land uses, topographic features, and raven management.

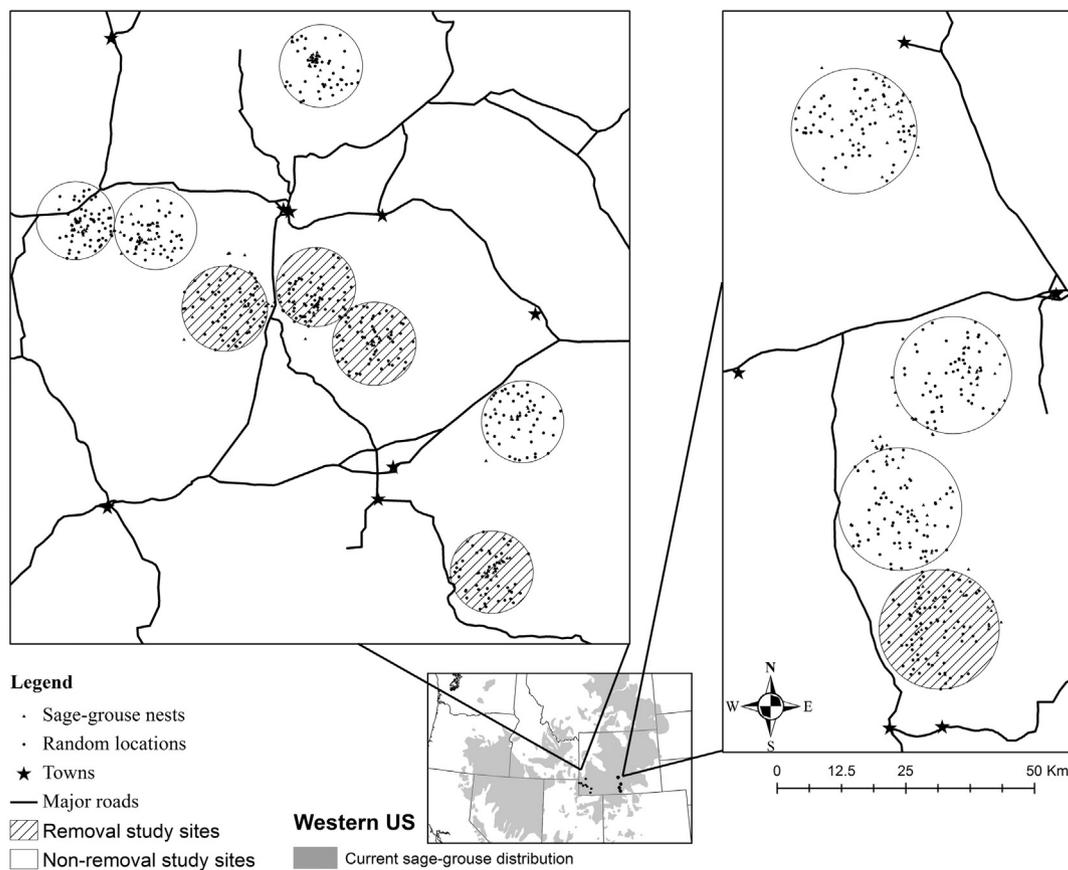
Removal and non-removal study sites had similar topographic features, weather, and vegetation. Elevation ranged from 1950 m to 2600 m among removal study sites and 1925 m to 2550 m among non-removal study sites. Most of the land within all of the study sites was federally owned and administered by the Bureau of Land Management (BLM) with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in the study sites. Overall annual coyote population reductions were similar between removal (annual range of number coyotes removed = 0.01–0.18 coyotes/km<sup>2</sup>) and non-removal (annual range of number coyotes removed = 0.0–0.15 coyotes/km<sup>2</sup>) study sites. All study sites had anthropogenic habitat modifications, which consisted mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction was present in two of the removal study sites and four of the non-removal study sites.

The dominant vegetation at all study sites was Wyoming big sagebrush (*A. tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), black sagebrush (*A. nova*), and little sagebrush (*A. arbuscula*). Other common shrub species included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), and spiny hopsage (*Grayia spinosa*). Juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were present at the higher elevations in isolated stands.

### 2.2. Sage-grouse capture and monitoring

During 2008–2011, we monitored sage-grouse hens during the nesting season (late-April to mid-July). Hens were captured, radio-collared, and released in April of each year. We captured hens at night using ATVs, spotlights, and hoop-nets (Connelly et al., 2003, Giesen et al., 1982, Wakkinen et al., 1992). Sage-grouse hens were fitted with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (Holohil Systems Ltd, RI-2D, Ontario, Canada or Advanced Telemetry Systems Inc, A4060, Isanti, MN, USA). We aged sage-grouse hens as yearlings or adults by examining outer primary feathers (Patterson, 1952), which we classified into a binary variable (AGE) designating 0 for adults and 1 for yearlings.

Late April through July 15, we located hens weekly with VHF receivers (Communications Specialists, R-1000, Orange, CA, USA) and 3-way Yagi antennas (Communications Specialists, Orange, CA, USA). The start date of nest monitoring was similar in date and timing after peak sage-grouse lek attendance among study sites and years to generate a relative assessment of nest success. Potential nests were identified with binoculars from >15 m by circling a radio-marked hen until she



**Fig. 1.** Location map of southern Wyoming depicting 8, 16-km diameter and 4, 24-km diameter study sites, southwestern and south-central, Wyoming, USA, 2008–2011. Magnified sections correspond on left to southwest and on right to south-central Wyoming. Map includes locations of 2008–2011 sage-grouse nests, random locations, landfills, towns, and major roads.

was visually spotted under a shrub. Nests were verified by triangulating the hen under the same shrub from  $\geq 100$  m away during all subsequent nest visits. We thoroughly searched the area of the potential nest when the hen was absent. We continued monitoring nests weekly until the nest hatched or failed. We assessed nest fate as successful or unsuccessful after a hen had left her nest. A successful nest was defined as having evidence that at least 1 egg hatched as determined by shell membrane condition (Wallestad and Pyrah, 1974).

### 2.3. Raven abundance monitoring

Between May 1 and August 1 of each year, we conducted point count surveys at random locations within each study site to compare raven densities. Random locations were selected in habitat considered to be available to sage-grouse for nesting within each study site. To restrict random locations to available nesting habitat, we used ArcMap 10.0 (ESRI Inc., Redlands, CA) to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest GAP landcover data from 2008 (Gap Analysis Program, 2008). Random locations were designated to be  $> 1000$  m apart; however, random selection led to average nearest neighbor distances among random point count locations of  $> 2000$  m. We generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year. Point-count methodology was consistent with the protocol described in Dinkins et al. (2012) and Dinkins (2013).

### 2.4. Predator removal

WS began lethally removing ravens in four of the five removal study sites in March 2007 and the fifth removal study site in February 2008.

Removal of ravens was conducted in response to livestock depredation; thus, WS removal activities were implemented at raven foraging areas and roosts near areas used by livestock (0–15 km; Table 1). WS removal activities were more focused on raven foraging areas (lambing and calving grounds and landfills) from February 2009 to June 2011 (Table 1).

WS personnel performed concentrated raven removal using DRC-1339 (3-chloro-p-toluidine hydrochloride) by treating 1.3-cm meat cubes or dog food or direct removal (i.e., shooting them with shotguns; Rod Merrell, personal communication); however, direct removal was uncommon (Carbon, Lincoln, Sweetwater, and Uinta counties four year total  $n = 57$  ravens). Typical WS raven removal methods entailed pre-baiting with non-treated bait for a few days to acclimate ravens to foraging on bait (meat cubes or dog food) before applying DRC-1339 to bait. The amount of DRC-1339 and bait applied at individual removal locations was proportional to the number of ravens WS personnel witnessed in that area. DRC-1339 concentration was applied as specified by the U.S. Environmental Protection Agency label ( $LD_{50} = 5.6$  mg/kg; Larsen and Dietrich, 1970).

Throughout Wyoming, coyotes have been lethally removed with aerial and ground methods by WS on an annual basis for the benefit of livestock and wildlife. There was spatial and temporal variability in the effort WS expended to reduce coyote populations in some of our study sites with most effort delegated to areas and years with complaints from livestock producers or sportsmen. However, WS consistently implemented an aerial and ground program to reduce the coyote population in 10 of our 12 study sites, albeit with a different effort within each study site by year. Lethal removal of coyotes was conducted by WS in all of the removal study sites and five of the seven non-removal study sites. We obtained data on the number of coyotes removed from areas encompassing our study sites from WS, which we

quantified as the annual number of coyotes removed per km<sup>2</sup> for each of our 12 study sites. For analyses on sage-grouse nest success, the quantification of the number of coyotes removed per km<sup>2</sup> was restricted to the winter and spring (November–April). We quantified the number of coyotes removed during these months to align with the time of year when snow was on the ground (WS was most successful at removing coyotes during this timeframe), when coyote populations were annually increasing, and removal efforts were directly before the sage-grouse nesting season. These data constitute an index of the relative abundance of coyotes within each study site among years, because we did not directly quantify the number of coyotes; at the very least, the number of coyotes removed was an index of the relative level of human manipulation of localized coyote populations. We do not suggest that this metric is indicative of the actual number of coyotes on the landscape.

### 2.5. 2.5. Climate variables

Climate variables used in nest success analyses included Palmer Z-index (PZI), average maximum temperature, and total precipitation. Palmer Z-index is an indicator of potential drought conditions, which we quantified for the previous winter and spring (winter PZI; November–April) and the current nesting season (nesting season PZI; May–July) at the spatial scale of climate regions. For Palmer Z-index, we used data from the National Climate Data Center (National Oceanic and Atmospheric Administration; <http://www.ncdc.noaa.gov/temp-andprecip/time-series/index.php>). Average maximum temperature and total precipitation variables were enumerated specific to each sage-grouse nest location relative to year. We obtained temperature and precipitation data from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) created by Oregon State University (<http://www.prism.oregonstate.edu/>). PRISM data were modeled using point-based climate data and a digital elevation map (Daly et al., 2000). Using ArcMap 10.0, we extracted average maximum temperature and total precipitation data surrounding sage-grouse nests at a 4-km spatial scale from PRISM GIS data layers for winter (November–March), nesting season (April–July), April, and the week before nest fate. Precipitation and temperature data in April corresponded to conditions prior to the sage-grouse nesting season. We also extracted 1-year lag values of PZI, temperature, and precipitation for winter, nesting season, April as a means to evaluate weather effects on residual grass cover.

### 2.6. Statistical analysis

Modeling of raven abundance and sage-grouse nest survival was conducted with an information theoretic approach (Anderson, 2008), and we compared models with Akaike's information criterion adjusted for sample size (AIC<sub>c</sub>) and Akaike weights ( $w_i$ ; Burnham and Anderson, 2002). We classified models  $>2 \Delta AIC_c$  compared to the null model as having moderate support, and models with  $>4 \Delta AIC_c$  compared to the null as having a greater degree of support (Arnold, 2010, Burnham and Anderson, 2002). We prevented multicollinearity by not including variables that co-varied in any model ( $r > 0.65$ ) as determined with a Pearson's correlation matrix. In this situation, we eliminated one co-varying variable from further analysis by retaining the variable that made the most biological sense.

#### 2.6.1. Raven density analysis

Function 'gdistcamp' in package UNMARKED version 2.1-1 (Fiske and Chandler, 2011) in R (R 3.0.2; R Development Core Team, 2015) was used to assess the annual abundance of ravens in removal and non-removal study sites by year or year trend. The 'gdistcamp' function fits a multinomial-Poisson mixture model (Royle et al., 2004) that allows for analysis of standard distance sampling data (Buckland et al., 2001, Ralph et al., 1995, Thomas et al., 2010) at discrete distance intervals, while simultaneously modeling covariates on detection and abundance (Fiske and Chandler, 2011). For 'gdistcamp' analyses, raven

detection distances were binned into 175-m intervals and right truncated at 1575 m. We chose distance intervals and truncation distances by determining the smallest interval and largest truncation distance that allowed for adequate fit of distance sampling models. Observation specific covariates on detection cannot be implemented with 'gdistcamp'; thus, we were unable to compare models with detection varying among observers. However, Dinkins et al. (2012) did not find differences in effective detection radius among observers on data collected for the first 3 years of this study. Thus, we did not incorporate differences in detection among observers into our 'gdistcamp' analyses.

We fit half-normal, hazard-rate, uniform, and exponential key detection functions with detection constant or varying by distance to the nearest power line (transmission or distribution), forested habitat, rural house, or oil and gas well, or topographic ruggedness (TRI) measured at 0.54, 1, and 3 km away from point count locations. Detailed explanations of these variables are provided in Dinkins et al. (2014). We selected the appropriate key detection function and compared models with and without covariates on detection using AIC<sub>c</sub>. The best data distribution of Poisson or negative binomial was also selected using AIC<sub>c</sub>. We adjusted 'gdistcamp' parameter estimates for survey effort (difference in the number of visits per point count location) by incorporating the number of visits per point count location as an offset, which is similar to the procedure used in Program DISTANCE (Thomas et al., 2010).

General annual raven abundance was modeled with year, year trend, and study site type (removal or non-removal) variables. Year and year trend variables were compared as single variable and additive models with study site type to assess which form of year (i.e., raven density different each year or trending greater or lower across time) best described raven density; thus, year and year trend were not combined in any single model. Models with an interaction between year or year trend  $\times$  study site type were assessed for the possibility of divergent raven abundance in removal and non-removal study sites. We used 95% confidence intervals (CI) to compare parameter estimates from top AIC<sub>c</sub> selected 'gdistcamp' models.

#### 2.6.2. Sage-grouse nest success analysis

We analyzed the effects of WS raven removal, number of coyotes removed, and weather variables on daily survival rate (DSR) of sage-grouse nests by fitting generalized linear models of DSR using maximum likelihood in Program MARK (White and Burnham, 1999). All variables were constructed at an annual temporal scale with only one value for each year that were spatially explicit by study site for raven removal and coyote removal numbers. Weather variable values were unique to each year, and spatially explicit to each nest.

To assess the effect of raven removal on sage-grouse nest DSR, we compared interactions between (1) year  $\times$  study site type, (2) year trend  $\times$  study site type, (3) removal study sites 2008 and 2009  $\times$  removal study sites 2010 and 2011  $\times$  non-removal study sites (raven reduction  $\times$  year), and (4) a null model. Upon completion of raven density modeling, we found raven densities in removal study sites to be high in 2008 and 2009 and lower in 2010 and 2011; whereas, raven densities in non-removal study sites were slightly greater in 2009–2011 compared to 2008 but were more similar across years than the removal study sites (see 3.1 for details). The raven reduction  $\times$  year comparison was intended to compare DSR of sage-grouse relative to when raven density at removal study sites was found to be higher versus lower in those study sites compared to DSR in non-removal study sites. Each of these interactive comparisons were direct assessments of the effect of WS removal activities at removal study sites on DSR of sage-grouse nests; thus, each of these interactions was evaluated separately and compared with AIC<sub>c</sub> to find the interaction that fit the data best.

We evaluated the effect of coyote removal numbers, winter PZI, nesting season PZI, precipitation (winter, nesting season, April, and last week hen on nest), and temperature (winter, nesting season, April, and last week hen on nest) on DSR of sage-grouse nests. Both

current year and 1-year lags were evaluated for PZI, precipitation, and temperature during winter, nesting season, and April. These variables varied within and between all study sites by year; thus, we incorporated them as continuous predictors of DSR. We also considered interactive effects between precipitation and temperature during the last week a hen was on her nest and coyote removal numbers. To reduce modeling complexity, we screened all continuous variables (85% CI of parameter estimates that did not overlap zero) to identify potentially informative variables as suggested by Arnold (2010). All possible combinations of the best AIC<sub>c</sub> selected raven removal model and informative continuous variables were compared. We used 95% CI to evaluate parameter estimates from our final models.

### 3. Results

We conducted 2930 point count surveys (1280 at removal and 1650 at non-removal study sites) during 2008–2011 at 660 random locations (287 removal and 373 non-removal study sites). Across all years, we counted 1068 ravens (646 at removal and 422 at non-removal study sites). The number of detected ravens was >60–80 detections, which Buckland et al. (1993) suggested was necessary for reliable density estimates. We found 124 sage-grouse nests (62 hatched and 62 depredated) in removal study sites and 243 sage-grouse nests (117 hatched and 121 depredated) in non-removal study sites.

#### 3.1. Raven density

Models with the hazard-rate key detection function, negative binomial distribution, and TRI at 540 m from point count locations were at least 10 AIC<sub>c</sub> lower than models with all other key detection functions and detection covariates. Rugged terrain was negatively associated with detection of ravens with a parameter estimate of TRI = -0.004 (95% CI: -0.008 to -0.0003). Average nearest WS removal activities were 10.95 km (0.28 SE) and 31.35 km (0.55 SE) away from point count locations and 14.5 km (0.4 SE) and 39.3 km (1.0 SE) away from nests within removal and non-removal study sites, respectively. There was large variation in the number of coyotes removed per km<sup>2</sup> (range = 0 to 0.18, mean = 0.04 [SE = 1.98]) among study sites and years.

The top AIC<sub>c</sub> ranked 'gdistamp' model was year × study site type ( $w_i = 0.84$ ; Table 2). The year × study site type interaction indicated that raven density at removal study sites decreased over time with the lowest raven densities within removal study sites during 2010 and 2011 (Fig. 2). In non-removal study sites, raven densities were similar across years but slightly lower in 2008 compared to 2009–2011 (Fig. 2). Raven densities in removal study sites were initially greater than densities in non-removal study sites (Fig. 2). This was expected because WS raven removal activities were only requested by livestock producers in areas with high densities of ravens. WS appeared to reduce high raven densities in removal study sites to densities observed in our non-removal study sites in 2010 and 2011 (Fig. 2).

**Table 1**

Number of removal events at (1) raven roost sites and foraging sites near livestock, (2) landfills, and (3) total number of removal events within 15 km of removal study sites. Raven removal was conducted by USDA/APHIS Wildlife Services in southwest and south-central Wyoming from January through June 2007–2011.

Year	Roosting/foraging	Landfill	Total
2007 <sup>a</sup>	11	0	11
2008	4	0	4
2009	30	5	35
2010	23	13	36
2011	17	5	22

<sup>a</sup> This was the only year with removal effort at roost locations ( $n = 5$ ).

**Table 2**

Multinomial-Poisson mixture models assessing the effect of year, year trend, and study site type (removal or non-removal) on raven densities using 'gdistamp' in R. Models were compared with Akaike's information criterion (adjusted for small sample sizes; AIC<sub>c</sub>) and Akaike weights ( $w_i$ ). Data were collected from 8, 16-km and 4, 24-km study sites in southwestern and south-central, Wyoming, USA ( $n = 287$  and 373 random point count locations for removal and non-removal study sites, respectively) during 2008–2011.

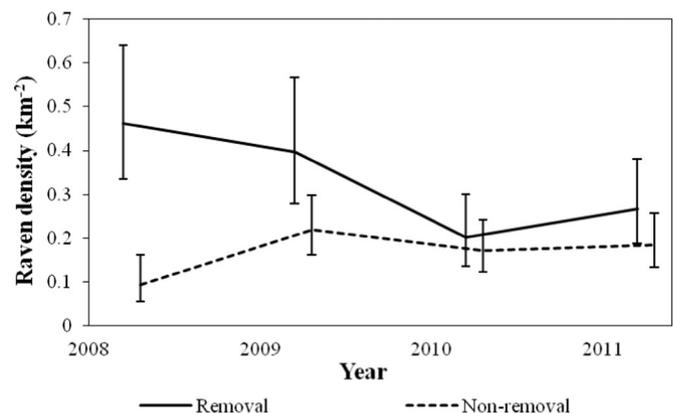
Models	K	ΔAIC <sub>c</sub>	$w_i$
Year × study site type <sup>a</sup>	12	0.00	0.84
Year trend × study site type	8	3.87	0.12
Year + study site type	9	8.19	0.01
Year trend + study site type	7	8.28	0.01
Study site type	6	8.78	0.01
Year	8	28.49	0.00
Year trend	6	28.58	0.00
Null	5	32.94	0.00

<sup>a</sup> AIC<sub>c</sub> = 4002.46.

#### 3.2. Sage-grouse nest success

For our evaluation of sage-grouse nest success relative to raven density reduction, the raven reduction × year was at least 3 ΔAIC<sub>c</sub> lower than year × study site type or year trend × study site type. Thus, we used raven reduction × year in additive models with continuous variables. Screening of continuous variables indicated that the 1-year lag variables, previous winter and current nesting season PZI and precipitation, current nesting season temperature, and coyote removal numbers × temperature during last week hen on nest were not informative parameters with 85% parameter estimates overlapping zero. Therefore, we did not include them in additive modeling. Winter temperature was an informative parameter with 85% CI that did not overlap zero; however, winter temperature was highly correlated with average April temperature (AprT;  $r > 0.65$ ), which fit the data better than winter temperature. We used AprT rather than winter temperature in additive modeling.

The best model describing DSR for sage-grouse nests included raven reduction × year, (AprT), temperature during last week hen on nest (Tweek), and coyote removal numbers × precipitation during last week hen on nest (coyote × week\_ppt) with  $w_i = 0.87$  (Table 3). In removal study sites while holding all continuous variables at the mean value, we found that DSR of sage-grouse nests was higher in 2010 and 2011 (0.976; 95% CI = 0.966 to 0.984) compared to 2008 and 2009 (0.951; 95% CI = 0.930 to 0.966) following reductions in raven density, which yielded cumulative nest success of 51.3% (95% CI = 38.2% to



**Fig. 2.** Raven density (no./km<sup>2</sup>) estimates by year, 2008–2011, from the top AIC<sub>c</sub> selected multinomial-Poisson mixture models for removal and non-removal study sites. Estimates of raven density were modeled from 287 and 373 random locations in removal and non-removal study sites, respectively. Error bars indicate 95% confidence intervals. Data were collected from four 16-km and one 24-km removal study sites and four 16-km and three 24-km non-removal study sites in southwestern and south-central, Wyoming, USA.

**Table 3**

Top 10 generalized linear models assessing daily survival rate of sage-grouse nests using Program MARK. Models were compared with Akaike's information criterion (adjusted for small sample sizes;  $AIC_c$ ) and Akaike weights ( $w_i$ ). Data were collected from 124 and 243 sage-grouse nests at removal and non-removal study sites, respectively. Sage-grouse were located in 8, 16-km and 4, 24-km study sites in southwestern and south-central, Wyoming, USA during 2008–2011.

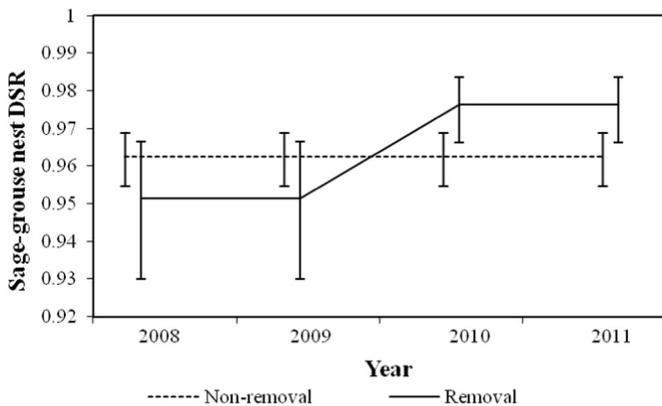
Models <sup>a</sup>	K	$\Delta AIC_c$	$w_i$
Raven reduction $\times$ year + coyote $\times$ week_ppt + AprT + Tweek <sup>b</sup>	8	0.00	0.87
Coyote $\times$ week_ppt + AprT + Tweek	6	4.81	0.08
Raven reduction $\times$ year + AprT + Tweek	5	6.04	0.04
AprT + Tweek	3	10.04	0.01
Raven reduction $\times$ year + coyote $\times$ week_ppt + AprT	7	13.04	0.00
Coyote $\times$ week_ppt + Tweek	5	17.11	0.00
Raven reduction $\times$ year + AprT	4	21.04	0.00
Tweek	2	24.31	0.00
Coyote $\times$ week_ppt + AprT	5	60.74	0.00
Raven reduction $\times$ year + coyote $\times$ week_ppt + AprT	7	61.69	0.00
Null model $AIC_c = 883.71$			

<sup>a</sup>  $AIC_c = 812.85$ .

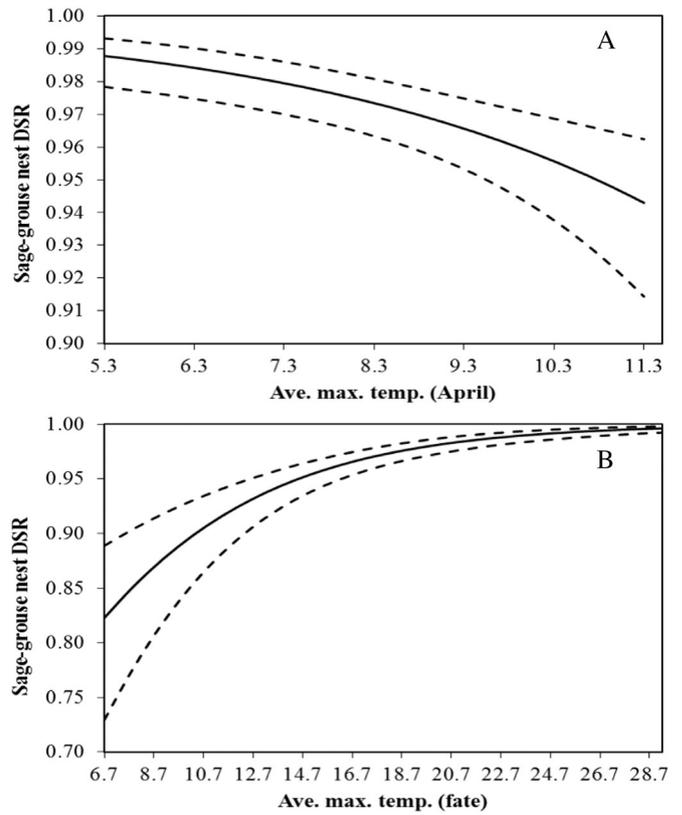
<sup>b</sup> Variables used to model DSR of sage-grouse included removal study sites 2008 and 2009  $\times$  removal study sites 2010 and 2011  $\times$  non-removal study sites (raven removal), coyote removal number per  $km^2 \times$  precipitation during last week hen on nest (Coyote  $\times$  week\_ppt), mean maximum temperature in April (AprT), and mean maximum temperature last week hen on nest (Tweek).

63.0%) and 24.8% (95% CI = 13.1% to 38.5%; Fig. 3) nest success estimates using a 28-day incubation period, respectively. Whereas, DSR remained stable across years in non-removal study sites, which yielded a 28-day nest success estimate of 34.2% (95% CI = 27.3% to 41.3%; Fig. 3).

In addition to raven reduction  $\times$  year, our best model indicated that temperature (AprT and Tweek) and precipitation (as interaction coyote  $\times$  week\_ppt) influenced DSR. Temperature had opposing effects on DSR with AprT negatively associated with DSR (parameter estimate =  $-0.26$ ; 95% CI:  $-0.39$  to  $-0.12$ ) and Tweek positively associated with DSR (parameter estimate =  $0.19$ ; 95% CI:  $0.14$  to  $0.24$ ; Fig. 4). Thus, nests exposed to cooler temperatures prior to the nesting season had higher success; whereas, failed nests were associated with cooler temperatures the week before the nest failed. Precipitation was only an informative variable as an interactive effect with coyote removal numbers (coyote  $\times$  week\_ppt parameter estimate =  $-0.55$ ; 95% CI:  $-0.99$  to  $-0.11$ ). This interactive effect indicated that nest success was substantially lower in areas with more coyotes removed and greater amounts of precipitation the week before the nest failed (Fig. 5).



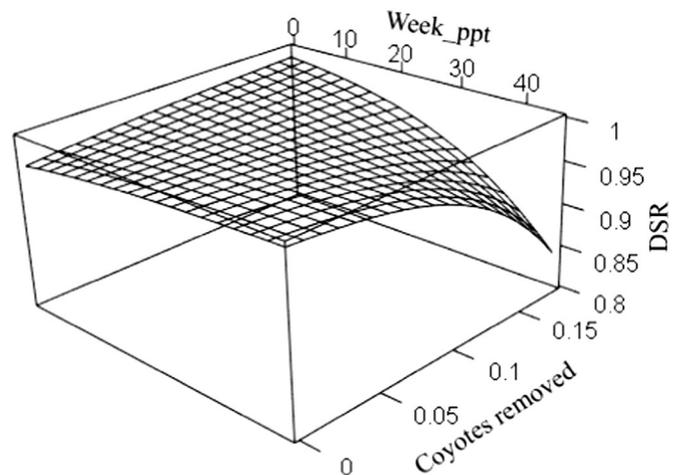
**Fig. 3.** Predictions of daily survival rate (DSR) of sage-grouse nests from the top  $AIC_c$  selected generalized linear model using Program MARK at removal and non-removal study sites. Predictions of DSR were generated from raven reduction  $\times$  year while holding all continuous variables at the mean value. Dashed lines represent 95% confidence intervals. Data were collected from 8, 16-km and 4, 24-km study sites in southwestern and south-central, Wyoming, USA ( $n = 367$  sage-grouse nests), 2008–2011.



**Fig. 4.** Predicted effects of (A) April temperature (AprT) and (B) temperature during last week hen on nest (Tweek) on daily survival rate of sage-grouse nests from the top  $AIC_c$  selected generalized linear model using Program MARK. Dashed lines represent 95% confidence intervals. Data were collected from 8, 16-km and 4, 24-km study sites in southwestern and south-central, Wyoming, USA ( $n = 367$  sage-grouse nests), 2008–2011.

**4. Discussion**

The negative effect of ravens on the nest success of birds has been well documented, including California least tern (*Sterna antillarum*; Avery et al., 1995), marbled murrelet (*Brachyramphus marmoratus*; Peery et al., 2004), sage-grouse (Coates et al., 2008, Bui et al., 2010,



**Fig. 5.** Predicted effects of coyote removal number per  $km^2$  (coyote removed/ $km^2$ )  $\times$  precipitation during last week hen on nest (Week\_ppt) on daily survival rate (DSR) of sage-grouse nests from the top  $AIC_c$  selected generalized linear model using Program MARK. Data were collected from 8, 16-km and 4, 24-km study sites in southwestern and south-central, Wyoming, USA ( $n = 367$  sage-grouse nests), 2008–2011.

Coates and Delehanty, 2010), sharp-tailed grouse (*Tympanuchus phasianellus*; Manzer and Hannon, 2005), and snowy plover (*Charadrius nivosus*; Burrell and Colwell, 2012). While we were unable to directly identify predators at sage-grouse nests, our evaluation of sage-grouse nest success relative to raven density reduction allowed us to evaluate the general effect of WS removal efforts on raven abundance and raven abundance on sage-grouse nesting success. Our study verified that WS raven management—as implemented from a practical logistics point-of-view—can reduce the abundance of ravens at a relatively large spatial scale (15-km radius or 706.5 km<sup>2</sup>, Fig. 2), and sage-grouse nest success increased in study sites that had raven densities reduced (Fig. 3). Differences in habitat quality among study sites likely explained much of the within year differences in sage-grouse nest success at each study site type. However, our comparison of relative nest success between non-removal and removal study sites—across a timeframe where raven density was decreased in removal study sites—allowed us to untangle how lethal removal of ravens influenced sage-grouse nesting success. Contrary to raven impacts on nesting birds, coyote abundance has not been associated with lower nest success nor has lethal removal of coyotes enhanced nest success or survival of ducks or sage-grouse (Orning, 2013, Prugh et al., 2009, Slater, 2003, Sovada et al., 1995). Predator removal, especially of an apex predator, such as the coyote, often has unintended consequences of reducing nest success of birds associated with increases in activity or abundance of smaller mammalian carnivores (mesopredators; Mezquida et al., 2006, Prugh et al., 2009, Sovada et al., 1995). However, lethally removing a combination of coyotes, raccoons, and ravens—with coyotes identified as the primary predator of eggs and chicks—increased the productivity of greater sandhill cranes (*G.c. tabida*) in Oregon (Littlefield, 2003).

Expansion and growth of raven populations in sagebrush habitat is likely to result in higher depredation rates on sage-grouse nests in localized areas (Bui et al., 2010, Coates and Delehanty, 2010, Evans, 2004). As sagebrush habitat is developed by humans, raven occupancy and density will increase in areas adjacent to and overlapping quality sage-grouse habitat (Leu et al., 2008, Howe et al., 2014). Anthropogenic structures in natural gas fields allowed for greater overlap of breeding ravens and sage-grouse nesting areas (Bui et al., 2010), and power lines provided nesting structure for ravens in sage-grouse habitat (Howe et al., 2014). Concomitantly, high-quality sagebrush habitat may become functionally unavailable to sage-grouse when raven densities are high (Dinkins et al., 2012, Dinkins et al., 2014). Several studies detailing predator-avoidance in birds indicate that the presence of a predator can have dramatic impacts on prey species use of habitat (Cresswell, 2008). Thus, quality nesting habitat for sage-grouse has become more limited from the loss of functional habitat, which has also resulted in more direct depredation of nests. In some areas, reductions in raven density at a landscape level may increase the amount of functional habitat for sage-grouse.

No WS removal activity was conducted within 1.1 km of a point count location during this study, which indicates that most breeding ravens within our study sites were unlikely to have been exposed to WS removal activities (e.g., breeding raven home range sizes: coastal California median home range radius = 0.62 km and Mojave Desert California average home range radius = 0.57 km [Boarman and Heinrich, 1999]). Breeding pairs of ravens actively forage close to their nests, which entails relying on natural food sources (including sage-grouse eggs) more than food subsidies associated with human activities (road-kill, dead livestock, and landfills). Thus, WS most likely removed transient ravens that traveled vast distances from roost to foraging sites. Kristan and Boarman (2003) found that densities of both breeding and non-breeding ravens were associated with increased predation of desert tortoises (*Gopherus agassizii*). Our results indicate that removal of primarily transient ravens resulted in increased sage-grouse nest success (Fig. 3). Thus, both breeding and transient ravens may contribute to sage-grouse nest failure with greater abundances of transient ravens possibly associated with incidental sage-grouse nest depredations.

In concordance with our weather based hypotheses, temperature effects on nest success were dependent on timing and likely associated with conditions promoting current year grass growth and odorants used by mammalian predators to search for sage-grouse. Higher temperatures prior to nesting likely lead to less grass growth during the nesting season for sage-grouse equating to less concealment cover, and grass height has been associated with greater nest success of sage-grouse (Doherty et al., 2014, Holloran et al., 2005). Higher temperatures break down odorants that mammalian predators use to detect prey (Conover, 2007, Gutzwiller, 1990, Ruzicka and Conover, 2012), and we found that nests with higher temperatures the week before nest fate were more likely to succeed (Fig. 4). However, sage-grouse hens may have had greater incubation consistency with warmer temperatures yielding lower likelihood of visual predators detecting nests. Lower temperatures and precipitation were positively associated with mesopredators detecting pseudo-nests in Utah (Ruzicka and Conover, 2012), and precipitation has been connected to lower nest success of wild turkeys (*Meleagris gallopavo*) attributed to higher nest depredation from olfactory predators (moisture-facilitated, nest-depredation hypothesis; Lehman et al., 2008, Roberts and Porter, 1998). Nest success during our study was substantially lower in areas with greater amounts of precipitation the week before the nest failed, but only when more coyotes were removed from that study site (Fig. 5).

Areas with human suppressed coyote numbers (i.e., more coyotes removed per km<sup>2</sup> by WS) did not have higher nest success; in fact, the lowest nest success for sage-grouse was in the study sites and years with the most coyote removal—when there was a greater amount of precipitation (Fig. 5). Mesopredators have been well documented to have greater negative effects on ground nesting birds compared to coyotes (Conover, 2007, Ruzicka and Conover, 2012, Sovada et al., 1995). Lethal removal can influence predator-prey dynamics by altering predator community structure and distribution, which has resulted in increased predation rates on bird nests (Greenwood et al., 1995). Coyotes have been documented as suppressing negative consequences of nest depredating mesopredators, such as badgers, raccoons, red fox, and skunks, on nest success (Mezquida et al., 2006, Prugh et al., 2009, Sovada et al., 1995). Our coyote removal numbers and precipitation interaction may be indicative of mesopredator release with increased reduction or manipulation of coyote abundance allowing mesopredators to increase in abundance or behaviorally expand their influence as predators of sage-grouse nests when precipitation was conducive to olfactory detection of sage-grouse nests (Fig. 5). Expansion of mesopredator home ranges resulting from suppression of coyote numbers is the most plausible explanation for study sites with annual increases in coyote removal; however, some study sites also exhibited continual coyote removal that may have resulted in increased abundance of mesopredators. This is mostly supposition, because we did not directly collect data on mammalian predator abundances. Therefore, more research on climatic variables and manipulation of predator communities is warranted.

The legitimacy of our use of the number of coyotes removed per km<sup>2</sup> was contingent on coyote removal being correlated with decreases in local coyote abundance. Within two of our study sites, Slater (2003) found that WS actually lowered the abundance of coyotes with increased removal effort. However, it was possible that study sites with no removal ( $n = 2$ ) had lower abundance of coyotes compared to areas with greater WS coyote removal numbers. We do not make any suggestion that this metric was indicative of the actual number of coyotes on the landscape but would be an index of the change in the relative number of coyotes (i.e., the number of coyotes removed was at least analogous to the level of artificial manipulation of the mammalian predator community). Thus, greater number of coyotes removed could have been realized as a reduction in the total mammalian predators on the landscape or could represent areas with greater shifts in the dominant mammalian predator—potentially to a predator community with more fox, badger, and raven. Total reduction in the mammalian

predator community would be related to decreased risk of nest depredation on sage-grouse. Whereas, predator community shift with increased nest depredation would be representative of mesopredator release, which is what we found when there was more precipitation in manipulated predator communities.

Lethal removal of ravens may be a potential mitigating strategy for areas of low sage-grouse nest success. Whereas, coyote abundance is dependent on prey availability, and humans attempt to reduce population size in many parts of Wyoming on an annual basis. Predator removal may provide a short-term release in predation rates within fragmented habitats and areas with subsidized predator populations (Bui et al., 2010, Coates, 2007, and Hagen, 2011). However, Hagen (2011) indicated that predator removal will not mitigate sage-grouse population declines throughout the range of sage-grouse. We agree that the positive effects of raven removal for sage-grouse nest success are likely short-lived gains. We monitored WS raven management as it was used to reduce raven depredation on livestock; thus, targeted raven management to benefit sage-grouse may produce better results. However, identification of areas where sage-grouse may benefit from raven removal and implementation of a raven removal program targeted at benefitting sage-grouse will not be an easy task. Management of both breeding and transient ravens will be necessary, which will present many challenges. Predator removal as an interim mitigation measure may have a place in sage-grouse management when sage-grouse populations are subjected to high densities of ravens. However, low reproductive rates may persist in many areas due to compensatory predation by other predators (Bui et al., 2010, Coates, 2007), and increasing nest success may not translate to increases in population size. Thus, long-term solutions to reduce human-subsidized raven populations are necessary to address potential negative effects of growing raven populations in sage-grouse habitat. Reducing raven abundance may be possible through non-lethal means, such as reducing availability of supplemental food (road-kill, dead livestock, and garbage) and nesting and perching structures (oil and gas structures, power lines, telephone poles, communication towers, etc.; Jiménez and Conover, 2001). More research needs to be focused on understanding raven population dynamics in sagebrush ecosystems, and how to reduce the utility of anthropogenic subsidies (food and nesting structure) for ravens.

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