

# Common ravens disrupt greater sage-grouse lekking behavior in the Great Basin, USA

**JOSEPH L. ATKINSON**, U.S. Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Drive, Suite D, Dixon, CA 95620, USA

**PETER S. COATES**, U.S. Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Drive, Suite D, Dixon, CA 95620, USA [pcoates@usgs.gov](mailto:pcoates@usgs.gov)

**BRIANNE E. BRUSSEE**, U.S. Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Drive, Suite D, Dixon, CA 95620, USA

**IAN A. DWIGHT**<sup>1</sup>, U.S. Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Drive, Suite D, Dixon, CA 95620, USA

**MARK A. RICCA**, U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 777 N.W. 9th Street, Suite 400, Corvallis, OR 97330, USA

**PAT J. JACKSON**, Nevada Department of Wildlife, 6980 Sierra Center Parkway, Suite 120, Reno, NV 89511, USA

**Abstract:** Expansion of human enterprise has contributed to increased abundance and distribution of common ravens (*Corvus corax*; ravens) across sagebrush (*Artemisia* spp.) ecosystems within western North America. Ravens are highly effective nest predators of greater sage-grouse (*Centrocercus urophasianus*; sage-grouse), a species of high conservation concern. Sage-grouse population trends are estimated using count survey data of males attending traditional breeding grounds, known as leks. We sought to investigate associations of ravens to sage-grouse lek sites and document interactions between the sage-grouse and ravens as well as those between sage-grouse and other animals observed around leks. First, we used extensive raven point counts and sage-grouse lek observation data collected across Nevada and California, USA, from 2009–2019 to evaluate spatial associations between sage-grouse and ravens while accounting for other environmental covariates. We found that ravens were more likely to be observed closer to lek sites, especially as leks increased in size. Second, we used a subset of the lek dataset from 2006–2019 to describe behavioral changes of male sage-grouse in the presence of ravens and other predators. Our analysis indicated that ravens are attracted to lek sites and were associated with disrupting lekking sage-grouse by causing flushes or ceasing displaying behaviors. These results suggest that adult and yearling sage-grouse perceive ravens as a reason to alter breeding activity, and ravens may adversely influence their reproduction during the lekking stage. Additionally, standardized techniques to count sage-grouse on leks for population trend analyses could be biased low if raven presence during surveys is not accounted for.

**Key words:** *Aquila chrysaetos*, California, *Centrocercus urophasianus*, common raven, *Corvus corax*, golden eagle, greater sage-grouse, interspecific aggression, lek, Nevada, predation, raptor

**DECLINING POPULATIONS** of greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) and concomitant loss and degradation of sagebrush (*Artemisia* spp.) ecosystems across the American West are focal points of local, state, and national conservation policy and efforts (U.S. Fish and Wildlife Service [USFWS] 2015). These declining trends have been ascribed to

a variety of natural and anthropogenic stressors that vary across sagebrush ecosystems (Aldridge et al. 2008, Conover and Roberts 2016), which include cropland conversion in the northern prairies (Connelly et al. 2004), energy development in the Wyoming Basin, USA (Harju et al. 2010), and an accelerated cycle of wildfire and annual grass invasion in the Great

<sup>1</sup>Present address: California Department of Fish and Wildlife, Upland Game Unit, 1010 Riverside Parkway, West Sacramento, CA 95605, USA.

Basin, USA (Coates et al. 2016a).

Predation by generalist predators is also recognized increasingly as a non-trivial threat to sage-grouse populations (Schroeder and Baydack 2001; Coates et al. 2008, 2020). Increasing common raven (*Corvus corax*; raven) and other generalist populations may have deleterious impacts on species of conservation concern (Boarman and Heinrich 1999, Boarman 2003). Raven populations have been bolstered particularly in the Great Basin owing to fragmentation of sagebrush ecosystems and associated anthropogenic resource subsidies (O'Neil et al. 2018; Coates et al. 2020, 2021a). These subsidies include energy infrastructure (e.g., transmission towers, lines, corridors) that provide substrates for nesting (Howe et al. 2014) and elevated perching (Coates et al. 2014) as well as cropland (O'Neil et al. 2018), high-density roads (O'Neil et al. 2018), livestock (e.g., watering sources; Coates et al. 2016b), and landfills (Kristan and Boarman 2007) that increase food availability.

Ravens are effective predators of sage-grouse nests (Holloran et al. 2005, Coates et al. 2008, Dinkins et al. 2012, Lockyer et al. 2013). They can adversely impact sage-grouse nest survival at broad spatial scales (Coates et al. 2020), which could limit population growth in areas where low nest survival is not compensated by higher rates in other life stages (e.g., chick survival). Female sage-grouse will often select nesting sites away from areas with high densities of ravens and other avian predators (Dinkins et al. 2012), though they still typically nest relatively close to their lek site (Connelly et al. 2004, Coates et al. 2013).

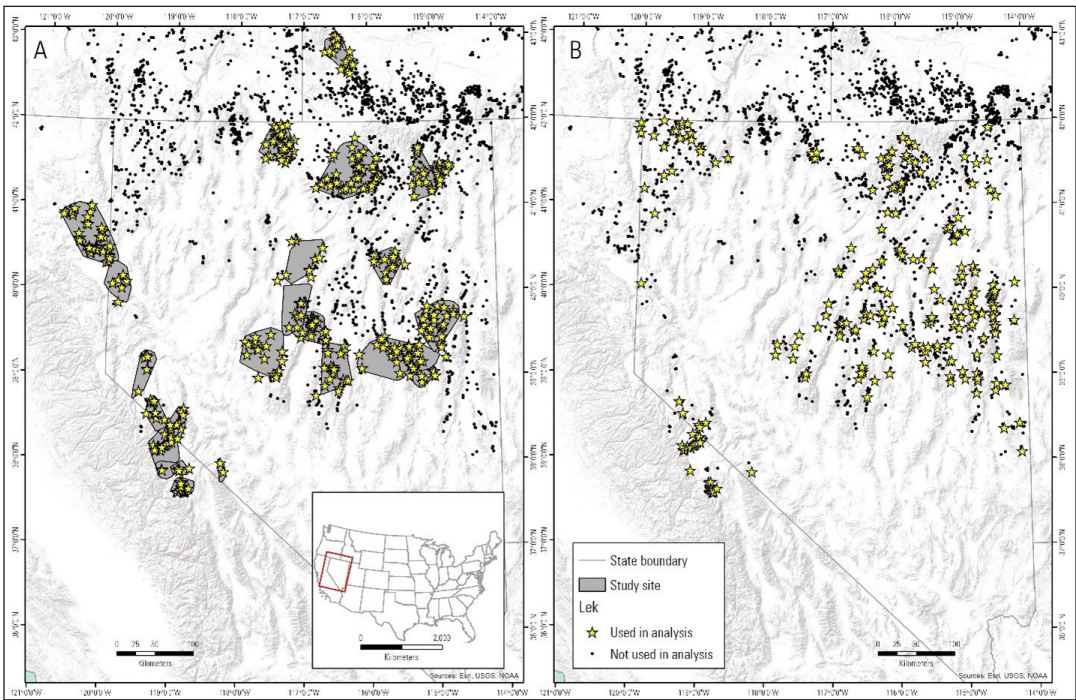
Prior to nesting, sage-grouse gather at traditional breeding sites, or leks, where males display and compete for mating opportunities with females (Schroeder et al. 1999). Few studies have empirically examined raven occurrence in proximity to leks, but evidence from a single study site suggests that ravens may be attracted to sage-grouse leks independent of anthropogenic resource subsidies (Coates et al. 2016b). Additionally, the co-occurrence of sage-grouse breeding areas with livestock or cropland further increases the probability of ravens on the landscape (Coates et al. 2016b). Other studies investigating raven occurrence across the landscape have generally focused on anthropogenic

subsidies, sage-grouse nesting habitat, or have otherwise not considered lek sites (Dinkins et al. 2012, Harju et al. 2018, O'Neil et al. 2018). Hence, understanding raven occurrence on a broad scale in relation to sage-grouse lek size and distance to lek could elucidate sources of disturbance impacting sage-grouse lekking activity and validate previous research (Coates et al. 2016b).

Importantly, sage-grouse have been shown to be sensitive to disturbance while lekking (Scott 1942, Hartzler 1974, Ellis 1984, Green et al. 2017, Muñoz et al. 2021, but see Bradbury et al. 1989), which could lead to short-term lek abandonment prior to counts or more cryptic behavior (e.g., not displaying or strutting) during counts. For example, elevated noise in proximity to leks can reduce attendance by males (Blickley et al. 2012), which has contributed to long-term lek abandonment in areas associated with energy infrastructure (Hess and Beck 2012, Green et al. 2017). The presence of non-native ungulates such as cattle (*Bos taurus*) and feral horses (*Equus ferus caballus*) on leks has also been shown to decrease activity on leks and increase the probability of flushing (Muñoz et al. 2021).

Counts of male sage-grouse attending leks are used widely to index population trends and estimate abundance locally, regionally, and rangewide (Connelly et al. 2003, Garton et al. 2011, Coates et al. 2021b). Like all survey methods, lek surveys are prone to sources of observation error, and there is an increasing recognition for the need to account for and understand these biases to achieve more reliable population estimates (Coates et al. 2019).

Accordingly, many studies have focused on how variation among environmental conditions (Baumgardt et al. 2017, Fremgen et al. 2018), sage-grouse movements (Blomberg et al. 2013, Fremgen et al. 2017, Wann et al. 2019), and survey estimation methodology (Monroe et al. 2016, Coates et al. 2019, Monroe et al. 2019) influence sage-grouse lek attendance rates and detectability, which can lead to incomplete or biased counts and resulting population trends. Alteration of lekking sage-grouse behavior, which can arise from perceived disturbance (Green et al. 2017) and risk of predation (Scott 1942, Hartzler 1974, Ellis 1984), could contribute to variation in observed counts and ultimately reduce lek persistence (Green et al. 2017).



**Figure 1.** Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) leks monitored in Nevada and eastern California, USA, 2006–2019 and utilized in (A) analyses investigating relationships of distance to lek and the probability of observing common ravens (*Corvus corax*; ravens) during point count surveys, and (B) analyses investigating sage-grouse lek behavior in response to ravens and other sage-grouse predators. Yellow stars represent surveyed leks utilized in the analysis, which included those leks nearest where raven point count surveys were conducted for analysis A, and those leks where abnormal lek behavior was noted for analysis B. Three surveys in analysis B were missing location coordinates and are not displayed on the map.

Disruption from predators is expected because displaying male sage-grouse are highly conspicuous, and peak lek activity occurs in open areas at first light and for a short period after sunrise, a behavior that may have evolved to better detect risk from predators (Gibson et al. 2002, Aspbury and Gibson 2004, Hagen 2011). The presence of predators at leks can cause sage-grouse to stop displaying, flush, and lower their subsequent attendance (Scott 1942, Hartzler 1974, Ellis 1984, Bradbury et al. 1989, Hagen 2011). Known predators of adult and yearling sage-grouse include coyotes (*Canis latrans*), golden eagles (*Aquila chrysaetos*), northern harriers (*Circus hudsonius*; Fletcher et al. 2003), prairie falcons (*Falco mexicanus*; Hartzler 1974, Conover and Roberts 2017), and large hawks in the genus *Buteo* (Schroeder et al. 1999, Fletcher et al. 2003, Hagen 2011, Conover and Roberts 2017).

Contrary to their efficacy as nest predators, ravens are not known to prey on adult or yearling sage-grouse (Conover and Roberts 2017).

However, sage-grouse nests are often located within 5 km of leks (Connelly et al. 2004, Coates et al. 2013), and ravens may be attracted to leks as a means of locating sage-grouse nest sites, a known food source for breeding ravens (e.g., Coates et al. 2008, Coates and Delehanty 2010, Howe and Coates 2015, Harju et al. 2021a).

The first objective of this study was to investigate the spatial association between ravens and active sage-grouse lek sites by evaluating raven survey data and lek count data collected across California and Nevada, USA, from 2009–2019. Based on observations reported in a previous study (Coates et al. 2016b), we predicted that ravens were more likely to be closer to sage-grouse leks than at random. Our rationale was that ravens can more easily locate nesting female sage-grouse near leks, especially if female sage-grouse visit the lek during the laying stage.

Our second objective was to investigate the influence of the presence of ravens and other sage-grouse predators at active leks on behaviors of male sage-grouse. We did this by lever-



aging existing recorded behavioral observations from a subset of lek surveys to estimate the probabilities of various causes of disturbance that induced changes in sage-grouse lek behavior. We predicted predators of adult and yearling sage-grouse would be more likely to induce behavioral changes, while responses of sage-grouse to ravens would depend on perceived threat. For example, we would expect fewer behavioral changes in response to the presence of ravens if sage-grouse tolerated raven harassment (Bradbury et al. 1989), whereas behavior would change (but potentially less so compared to predators of adults and yearlings) if sage-grouse perceived ravens as a threat. Finally, we present photographic and video-recorded evidence of direct interactions between ravens and sage-grouse on leks, showing multiple ravens attacking individual sage-grouse and exhibiting aggressive behaviors.

### Study area

The study area included field sites throughout sage-grouse distribution in Nevada as well as sites in a disjunct area along the California-Nevada border (Figure 1). This geographic extent covers much of the species' range in the Great Basin. Importantly for sage-grouse conservation, this includes the Bi-State Distinct Population Segment (DPS) along the California and Nevada border. Sage-grouse in the Bi-State DPS are genetically different from other populations of sage-grouse, though their behavior is not (Oyler-McCance et al. 2015), and lek behavioral data can thus be compiled with that of sage-grouse from other parts of their range.

## Methods

### Data collection

*Raven lek distance analysis.* The Western Association of Fish and Wildlife Agencies (WAFWA) provided a comprehensive database of lek count data used for this analysis. Sage-grouse lek counts were completed across Nevada and California, 2009–2018, using established lek count protocols by the California Department of Fish and Wildlife, Bureau of Land Management (BLM), U.S. Forest Service (USFS), and U.S. Geological Survey (USGS). Observers on the ground conducted lek counts 30 minutes before to 90 minutes after sunrise using binoculars and spotting scopes from early March through late April

to capture peak lek attendance by males (Monroe et al. 2016, Wann et al. 2019). Sage-grouse will typically leave the lek between 30 minutes and 90 minutes after sunrise (Jenni and Hartzler 1978), and numbers of sage-grouse counted typically peak around sunrise (Monroe et al. 2016). During each survey, observers recorded 3 separate counts of males on the lek, and the highest count was retained.

For leks that were monitored multiple times each year (average number of lek counts per year = 2.3, SD = 1.8), the maximum male count was assumed to represent peak male attendance for each lek during that year. Because all leks were not counted in every year, for the purposes of this analysis, we averaged peak male attendance across years monitored to obtain an average lek size. Measures of quality assurance and quality control were conducted prior to analysis (WAFWA 2015).

In addition to lek counts, we carried out raven point count surveys at our field sites across California, Idaho, and Nevada, USA (Figure 1), during daylight hours from March through July, 2009–2019, to represent peak lekking and nesting activity for sage-grouse. We did not subset raven point count surveys based on time of day when lekking occurs because ravens may be attracted to lekking areas as hubs of sage-grouse nesting activity (Connelly et al. 2004, Coates et al. 2013). We conducted surveys within sagebrush-dominated environments on lands administered by BLM, USFS, state agencies, or private stakeholders. During a 10-minute point count, observers documented all raven observations and distance to observed ravens. For the purposes of this analysis, we considered ravens to be present at the survey if 1 or more ravens were observed and absent if no ravens were observed during the survey. We also removed observations at distance from the observer >1,225 m to avoid misidentification at large distances. We then calculated distance to nearest active lek (i.e., at least 2 males observed during at least 2 years; Coates et al. 2021b) for each raven survey point location, and because we were interested in the effects of leks on the probability of observing ravens, we subset the data to include only those surveys within the 95<sup>th</sup> percentile of distances from leks (12.8 km). The 12.8-km distance around leks likely represents the more rural areas surrounding them.



**Figure 2.** Common raven (*Corvus corax*) pulling on greater sage-grouse (*Centrocercus urophasianus*) tail, Mono County, California, USA, March 20, 2018 (photo courtesy of M. Tracy, Bureau of Land Management).

Beyond that distance, factors such as anthropogenic development may have greater influence on raven occurrence.

*Lek disturbance analysis.* To examine causes of disturbance that induced changes in lekking behaviors of sage-grouse, we conducted a post hoc analysis using a subset of lek count surveys collected by USGS, BLM, and the Nevada Department of Wildlife in Nevada and California from 2006–2019 (Figure 1B). Surveys were spaced approximately 2 weeks apart to capture the distribution of attendance. Specifically, we included only lek surveys where changes in sage-grouse lekking behaviors were noted that indicated disturbance, including stopping displaying or flushing from the lek. We categorized behavioral observations as “not displaying” when sage-grouse were present during the survey but noted explicitly as crouching, standing, or feeding while on the lek, and not showing any displaying behavior. We categorized behavioral observations as “flush” when sage-grouse flew away from the lek site during the survey. We combined behavioral observations categorized as “flush” or “not display” into a third “combined” category, which also included surveys where behavioral changes were noted, but not specified. We only included surveys where over half the sage-grouse attending the lek exhibited changes in lekking behavior (e.g., flush), which allowed our analyses to be

conducted at the lek level rather than at the individual level. We also excluded surveys where observers noted that their approach changed sage-grouse behavior. Furthermore, we did not include lek surveys without male sage-grouse present because it was impossible to determine what caused the males to be absent (e.g., inactive leks or recent flushing), and we discarded observations that did not follow standardized protocols (Connelly et al. 2003). For each lek-count level behavioral observation, we categorized the disturbance that induced change in lekking behavior.

Surveyors were trained in raptor identification and used the same equipment used to count grouse to identify causes of disturbance. Disturbances included: ravens, coyotes, golden eagles, other raptors, inclement weather, native ungulates, and non-native ungulates. Lek counts where no disturbance cause was noted, such as when grouse naturally stop displaying or flush from the lek after sunrise, or where multiple possible causes were noted, were classified as unknown.

Our final dataset consisted of 464 lek count surveys in Nevada ( $n = 379$ ) and California ( $n = 85$ ) during 2006–2019. We found 6,540 surveys documented the presence of grouse on the lek during the survey within the analyzed years. We discarded most of these surveys due to insufficient data regarding disturbed lekking behavior. During 2 lek surveys, researchers documented interactions between ravens and sage-grouse (Figure 2; Appendix A). Both the photograph and the video recordings were opportunistically taken.

## Statistical analyses

*Raven lek distance analysis.* We used generalized linear mixed effects models (binomial error distribution; Zuur et al. 2009), which allowed us to examine if ravens selected areas closer to lek sites in a logistic regression framework with a logit link function, following methods described in Coates et al. (2016b). This model took the form:

$$\text{logit}(Y) = \beta_0 + X\beta + \eta \quad (1)$$

where  $\beta_0$  represents the intercept,  $X$  is a matrix of fixed effect covariates,  $\beta$  is a vector of selection coefficients, and  $\eta$  is a random intercept for year (Gillies et al. 2006). We included the year

random effect to account for temporal autocorrelation. Observations ( $Y$ ) followed a Bernoulli distribution, with  $Y = 1$  indicating surveys where at least 1 raven was observed and  $Y = 0$  indicating surveys where ravens were not observed.

To account for other landscape characteristics previously found to influence raven occupancy, in all our models we included parameters from O'Neil et al. (2018) with main effects that had credible limits (CrL) not overlapping 0 at 68%. These included road density within 3,590 m (U.S. Census Bureau 2015), intermittent stream density within 1,450 m (USGS 2017b), vegetation greenness index (normalized difference vegetation index; NDVI; Land Processes Distributed Access Archive Center 2017) within 1,450 m, elevation (USGS 2009), proportion of big sagebrush within 3,590 m (Comer et al. 2002), proportion of shrub open edges within 3,590 m (Comer et al. 2002, Homer et al. 2015, USGS 2017a), and exponential distance to agriculture (Comer et al. 2002, Leu et al. 2008). We excluded exponential distance to roadside rests because 96% of raven surveys used in this analysis were >12.8 km from roadside rests and <1% were within 6.9 km, or the average daily movement of ravens (Engel and Young 1992). Exponential distances were calculated using the following equation:

$$\exp\left(-\frac{d}{\alpha}\right) \quad (2)$$

where  $\alpha$  was the mean distance to the landscape feature from locations where ravens were observed. We conducted computations of land cover characteristics using zonal statistics tools within ArcGIS 10.4 (Environmental Systems Research Institute, Redlands, California, USA).

We chose to use a maximum likelihood approach for this analysis so that we could compare support across multiple models using Akaike's information criterion with second-order correction ( $AIC_c$ ; Anderson 2008). Our final model set consisted of models comparing covariates representing linear and exponential distance to leks as well as additive effects and interactions of distance to lek with average lek size of the nearest lek. We included interactions of distance to lek with average lek size of the nearest lek to estimate if ravens were more likely to select areas closer to larger leks.

To account for other landscape characteristics known to influence raven occupancy, all models included the parameters obtained from O'Neil et al. (2018), and we included a baseline model (i.e., including only covariates from O'Neil et al. 2018) to compare support for the additional covariates describing selection for leks. We report results from the best supported model (i.e., lowest  $AIC_c$ ), including mean parameter estimates ( $\beta$ ), 95% and 85% confidence intervals (CI). We considered parameters with 95% CI not overlapping 0 to have substantial support from the data, and those with 85% CI not overlapping 0 to have moderate support. We conducted this analysis using "lme4" (Bates et al. 2020) within Program R version 4.0.2 (R Development Core Team 2020).

*Lek disturbance analysis.* For this analysis, our objective was to estimate probabilities of different causes of disturbance resulting in changes in sage-grouse lek behavior. We did not differentiate numbers of a given disturbance and simply analyzed based on presence or absence for each disturbance. For each sage-grouse behavior that we were interested in (i.e., flush, not display, and combined), we estimated the probabilities for each of the causes of disturbance, while accounting for temporal autocorrelation. We chose a Bayesian framework over a maximum likelihood estimation framework because it allowed us to estimate probabilities and uncertainty of multiple causes of disturbance within a single model as opposed to the previous analysis where we compared multiple competing models using  $AIC_c$ . Here, we employed a Bayesian multinomial logistic model (Darrach et al. 2017, Muñoz et al. 2021), which took the following form:

$$y_i \sim \text{multinomial}([P_{RAVi}, P_{COYi}, P_{EAGi}, P_{RPTi}, P_{WEAi}, P_{UNGi}, P_{UNKi}], 1) \quad (3)$$

with  $y$  representing causes of disturbance at lek  $i$  using a multinomial distribution such that an observation of lek  $i$  will have only 1 cause: ravens ( $RAV$ ), coyotes ( $COY$ ), golden eagles ( $EAG$ ), other raptors ( $RPT$ ), inclement weather ( $WEA$ ), ungulates ( $UNG$ ), or unknown ( $UNK$ ). Ravens were used as the reference category, and we calculated the likelihood of all other disturbance categories ( $DIST$ ), which took the general form of:

$$\eta_{DISTi} \sim \beta_0 + \kappa_j \tag{4}$$

where  $\eta_{DISTi}$  is the probability of each cause of disturbance at lek  $i$ . The intercept  $\beta_0$  represents the average rate of each disturbance while  $\kappa_j$  represents a random effect of year to account for temporal autocorrelation on rates of each disturbance at lek  $i$ . The probability of each disturbance category then follows the logit function:

$$P_{DISTi} = \frac{e^{\eta_{DISTi}}}{1 + \sum e^{\eta_{DISTi}}} \tag{5}$$

For the reference category (i.e., ravens), the probability was calculated as:

$$P_{RAVi} = \frac{1}{1 + \sum e^{\eta_{DISTi}}} \tag{6}$$

For each of 3 separate multinomial analyses estimating the probabilities of causes of disturbance when sage-grouse lek behavior changes were noted (flushed, not display, and combined), we conducted analyses in “rjags” version 4.10 (Plummer et al. 2019) within Program R version 4.0.2 (R Development Core Team 2020). We used the “gelman.diag” function in the “coda” package (version 0.19-4; Plummer et al. 2016) to observe convergence. Each model took different amounts of iterations and burn-in to converge. For the flushed, not display, and combined models, we ran 3 chains, each

with 160,000, 140,000, and 30,000 iterations after burn-ins of 200,000, 100,000, and 20,000 and thinning factors of 20, 20, and 5, respectively. We used uninformative priors for all parameters. We present median probabilities and 95% CrL, unless otherwise stated.

## Results

### Raven lek distance analysis

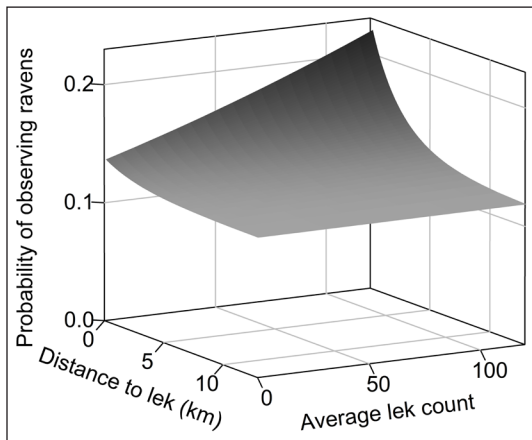
We used 21,160 raven point count surveys within this analysis. We identified the nearest lek to each raven point count survey, which identified 337 individual leks, ranging in size from 1–122 males counted (average = 17). Overall probability of observing ravens during a 10-minute survey was 0.10 (95% CI = 0.09–0.12). We found strongest evidence for the model including an interaction of the exponential decay variable representing distance to nearest lek with average lek size of the nearest lek (Table 1). We found that ravens were closer to leks overall, but the effect of distance varied by lek size (i.e., interaction effect; Table 1; Figure 3). For example, the probability of observing ravens at a survey was highest nearest to leks with a greater average number of grouse (Figure 3). Although the 95% CI of the interaction slightly overlapped 0 (Table 2; Figure 3), the 85% CI did not overlap 0, indicating moderate support from the data. We also found substan-

**Table 1.** Generalized linear mixed effects model results examining the relationship between probability of observing common ravens (*Corvus corax*; ravens) during 10-minute point count surveys and distance to greater sage-grouse (*Centrocercus urophasianus*) leks within Nevada and California, USA, 2009–2019. All models included all first-order effects that were found to influence raven occurrence from O’Neil et al. (2018)<sup>a</sup>.

Parameters	K	AICc	ΔAICc	AICc wt.
Exponential distance to lek * average lek size	12	16,141.8	0.0	0.46
Exponential distance to lek + average lek size	11	16,142.0	0.2	0.42
Linear distance to lek * average lek size	12	16,146.1	4.3	0.05
Exponential distance to lek	10	16,146.7	4.9	0.04
Linear distance to lek + average lek size	11	16,147.8	6.0	0.02
Linear distance to lek	10	16,152.2	10.4	0.00
Average lek size	10	16,152.8	11.0	0.00
Baseline model	9	16,157.6	15.8	0.00

<sup>a</sup> Road density within 3,590 m, intermittent stream density within 1,450 m, vegetation greenness index within 1,450 m, elevation, proportion of big sagebrush (*Artemisia* spp.) within 3,590 m, proportion of shrub open edges within 3,590 m, and exponential distance to agriculture.





**Figure 3.** Interaction effect of average greater sage-grouse (*Centrocercus urophasianus*) lek count and distance to lek from generalized linear mixed effects models examining the probability of observing common ravens (*Corvus corax*) during 10-minute point count surveys within Nevada and California, USA, 2009–2019. For the figure, all other variables in the model were held at their mean value.

tial evidence (95% CI not overlapping 0) that ravens were more likely to select relatively low elevation sites with greater road densities within 3,590 m, greater proportion of shrub, and open edges within 3,590 m (Table 2). In addition, we found substantial evidence for exponential distance effects to agriculture, where the probability of observing ravens was higher closer to agriculture (Table 2). We did not find evidence (i.e., 85% CI overlapped 0) for effects of intermittent streams or NDVI.

### Lek disturbance analysis

We classified causes of disturbance resulting in changes in sage-grouse lek behavior at 464 lek count surveys. We observed predators at leks sites in 97 of the 464 (20.9%) counts where changes in behavior were observed (Table 3). Ravens were the most prevalent predator ( $n = 33$  surveys), followed by other raptors ( $n = 23$ ), coyotes ( $n = 22$ ), and golden eagles ( $n = 19$ ). Other raptors included unidentified raptors ( $n = 9$ ), northern harriers ( $n = 6$ ), red-tailed hawks (*B. jamaicensis*;  $n = 4$ ), ferruginous hawks (*B. regalis*;  $n = 2$ ), rough-legged hawks (*B. lagopus*;  $n = 1$ ), peregrine falcons (*Falco peregrinus*;  $n = 1$ ), prairie falcons ( $n = 1$ ), and bald eagles (*Haliaeetus leucocephalus*;  $n = 1$ ); a northern harrier and a red-tailed hawk were both present during 1 survey and a northern harrier and a

prairie falcon were both present during another survey. Native ungulates were observed at 26 of 464 analyzed lek surveys, and introduced ungulates were observed at 14 lek surveys. Native ungulates included pronghorn (*Antilocapra americana*;  $n = 19$  surveys), mule deer (*Odocoileus hemionus*;  $n = 6$ ), and elk (*Cervus canadensis*;  $n = 1$ ); pronghorn and mule deer were both present at a single analyzed lek survey. Introduced ungulates included cows ( $n = 7$ ) and feral horses ( $n = 7$ ). Inclement weather, especially wind and precipitation, was the noted cause of behavior changes at 40 lek surveys. Additionally, we classified 288 lek surveys as “unknown,” which likely included instances of typical pauses in lekking behavior by males and instances of birds leaving leks after sunrise.

Ravens were the most common predator associated with disturbance (median = 0.07, 95% CrL: 0.05–0.10). Ravens were more likely to be associated with flush events (median = 0.08, 95% CrL: 0.04–0.13) over not display events (median = 0.06, 95% CrL: 0.03–0.09). Additionally, ravens were associated with flush at similar rates to golden eagles and coyotes (Table 3). Golden eagles were observed disturbing leks (median = 0.04, 95% CrL: 0.02–0.07) at similar levels as other raptors (median = 0.04, 95% CrL: 0.02–0.07) and coyotes (median = 0.04, 95% CrL: 0.02–0.07). However, golden eagles caused comparably high levels of flushing (median = 0.09, 95% CrL: 0.04–0.17) but never caused sage-grouse to stop displaying (median = 0.00, 95% CrL: 0.00–0.00).

In addition to predators, other disturbances, such as inclement weather and ungulates, caused disruptions in sage-grouse lekking behavior (Table 3). Inclement weather was the most commonly known reason for sage-grouse to not display (median = 0.10, 95% CrL: 0.04–0.17), though the effects of weather on flushing were very minimal (median = 0.00, 95% CrL: 0.00–0.01). Ungulates were associated with a similar level of disturbance (median = 0.08, 95% CrL: 0.05–0.12) to inclement weather, though they were associated with more flushing events (median = 0.10, 95% CrL: 0.03–0.18) and fewer not display events (median = 0.06, 95% CrL: 0.03–0.11). Sage-grouse ceased displaying for unknown reasons (median = 0.73, 95% CrL: 0.64–0.83) and flushed for unknown reasons (median = 0.60, 95% CrL: 0.48–0.71); overall,



**Table 2.** Parameter estimates with standard error and 95% confidence limits from generalized linear mixed effects models examining the relationship between probability of observing common ravens (*Corvus corax*) during 10-minute point count surveys and distance to greater sage-grouse (*Centrocercus urophasianus*) leks within Nevada and California, USA, 2009–2019. Excluding exponential distances, all parameters were standardized prior to modeling.

Parameters	$\beta$	SE	85% CI	95% CI
Exponential distance to nearest lek	0.3	0.08	0.18–0.41	0.14–0.45
Average lek count of nearest lek	-0.001	0.05	-0.07–0.07	-0.09–0.09
Exponential distance to lek * average lek count	0.12	0.08	0.004–0.24	-0.04–0.29
Exponential distance to agriculture	0.41	0.09	0.28–0.53	0.23–0.58
Elevation	-0.21	0.03	-0.25 to -0.17	-0.27 to -0.16
Proportion of shrub open edge within 3,590 m	0.11	0.02	0.08–0.14	0.07–0.15
Road density within 3,590 m	0.11	0.02	0.08–0.14	0.07–0.15
Proportion big sagebrush within 3,590 m	0.07	0.02	0.03–0.1	0.02–0.11
Greenness index within 1,450 m	-0.002	0.03	-0.04–0.04	-0.06–0.05
Intermittent stream density within 1,450 m	-0.03	0.03	-0.07–0.01	-0.08–0.03

sage-grouse were observed leaving the lek or ceased displaying for unknown reasons during nearly two-thirds of our analyzed surveys (median = 0.64, CrL: 0.57–0.72). Probability distributions for each model are described in Table 3, with associated model parameter coefficients described fully in Appendix B.

Video evidence provided in Appendix A captured ravens flushing the lek by flying over and calling (Appendix A). Furthermore, Figure 2 provides evidence of ravens harassing male sage-grouse at a lek. Specifically, several ravens were observed surrounding a displaying male sage-grouse and pulling its tail feathers; shortly thereafter, the lek flushed.

## Discussion

The effects of predators across sage-grouse life-history stages represent an information gap garnering increased attention (Dinkins et al. 2012, O’Neil et al. 2018) and is especially important in the Great Basin, which comprises >40% of the current range-wide sage-grouse population (Schroeder et al. 2004). Although ravens are a well-documented sage-grouse nest predator (e.g., Holloran et al. 2005, Coates et al. 2008, Lockyer et al. 2013, Howe and Coates 2015), nonlethal effects of ravens on sage-grouse lekking behavior have not been quantified previously as described heretofore.

Based on our findings, ravens appear to favor areas near lek sites. Though previous research

evidenced a linear relationship with raven distance to lek at a site-specific scale (Coates et al. 2016b), our models supported an exponential relationship based on data across multiple study areas. Therefore, the curvilinear relationship found here is an extension of previous findings and represents a broad-scale phenomenon that ravens select areas in close proximity to leks. Further, our model results indicate that ravens’ attraction to leks increases with increasing lek size (Figure 3). Ravens may be attracted to greater numbers of displaying male sage-grouse because they provide greater audio and visual cues that likely alert ravens to lek locations (Conover et al. 2010). Additionally, larger leks likely have higher female attendance and thereby provide more opportunities for ravens to find nearby nests (Holloran et al. 2005, Coates et al. 2008, Lockyer et al. 2013, Howe and Coates 2015, Harju et al. 2021a), especially considering sage-grouse typically nest in close proximity to leks (Connelly et al. 2004, Coates et al. 2013).

Specifically, ravens may be using leks as a point from which to search for nearby nests, and larger lek sizes equates to greater concentrations of nesting females. Thus, attraction to leks may be a signal that ravens are cueing into potential food sources (Howe and Coates 2015, Harju et al. 2021a), particularly during times of scarcity at the end of winter when sage-grouse begin nesting and other prey are less available (Coates and Delehanty 2010).

**Table 3.** Lek count observations ( $n = 464$ ) classified by greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) behavior in response to different disturbances at 250 leks within Nevada and California, USA, 2006–2019. Median predicted estimates and 95% credible limits (CrL) estimated using a Bayesian multinomial logistic regression model describing sage-grouse lekking behaviors in the presence and absence of various predators from 250 leks monitored in California and Nevada, 2006–2019.

Disturbance	Behavior <sup>a</sup>	$n$	Median	CrL	
				Lower (0.025)	Upper (0.975)
Raven ( <i>Corvus corax</i> )	Combined	33	0.07	0.05	0.10
	Not display	14	0.06	0.03	0.09
	Flush	12	0.08	0.04	0.13
Coyote ( <i>Canis latrans</i> )	Combined	22	0.04	0.02	0.07
	Not display	6	0.01	0.00	0.04
	Flush	13	0.08	0.03	0.14
Golden eagle ( <i>Aquila chrysaetos</i> )	Combined	19	0.04	0.02	0.07
	Not display	0	0.00	0.00	0.00
	Flush	15	0.09	0.04	0.17
Other raptors <sup>b</sup>	Combined	23	0.04	0.02	0.07
	Not display	10	0.03	0.00	0.07
	Flush	10	0.04	0.00	0.10
Inclement weather	Combined	40	0.08	0.04	0.12
	Not display	29	0.10	0.04	0.17
	Flush	4	0.00	0.00	0.01
Ungulates <sup>c</sup>	Combined	39	0.08	0.05	0.12
	Not display	17	0.06	0.03	0.11
	Flush	18	0.10	0.03	0.18
Unknown <sup>d</sup>	Combined	288	0.64	0.57	0.72
	Not display	174	0.73	0.64	0.83
	Flush	92	0.60	0.48	0.71

<sup>a</sup> In addition to leks noted as “not display” or “flush,” “combined” includes leks that were clearly disturbed, but not clearly defined as either “not display” or “flush.”

<sup>b</sup> “Other raptors” includes northern harriers (*Circus hudsonius*;  $n = 6$  surveys), red-tailed hawks (*Buteo jamaicensis*;  $n = 4$  surveys), ferruginous hawks (*B. regalis*;  $n = 2$  surveys), rough-legged hawks (*B. lagopus*;  $n = 1$  survey), peregrine falcons (*Falco peregrinus*;  $n = 1$  survey), prairie falcons (*F. mexicanus*;  $n = 1$  survey), bald eagles (*Haliaeetus leucocephalus*;  $n = 1$  survey), and unidentified raptors ( $n = 9$  surveys). One survey had both a northern harrier and a prairie falcon; another survey had both a northern harrier and a red-tailed hawk.

<sup>c</sup> Ungulates included pronghorn (*Antilocapra americana*;  $n = 19$  surveys), feral horses (*Equus ferus caballus*;  $n = 7$  surveys), domestic cattle (*Bos taurus*;  $n = 7$  surveys), mule deer (*Odocoileus hemionus*;  $n = 6$  surveys), and elk (*Cervus canadensis*;  $n = 1$  survey).

<sup>d</sup> Multiple factors were present during 35 lek surveys.

While ravens are not known to depredate adult or yearling sage-grouse, the presence of ravens at and around leks likely has adverse effects on sage-grouse reproductive behavior. Results from our lek disturbance models indicated that ravens impacted sage-grouse lekking behavior, suggesting sage-grouse may perceive

ravens as a non-trivial threat. Anecdotally, we have observed ravens directly harassing sage-grouse at lek sites (Figure 2) and exhibiting aggressive behaviors such as tail-pulling, divebombing, and mobbing, in addition to disruption of sage-grouse display behaviors, such as flushing them from their breeding grounds

(Appendix A). Ravens have also been observed pulling rectrices of female sage-grouse on their nests (Schroeder et al. 1999; B. G. Prochazka, USGS, personal communication), and similar tail-pulling has been documented between ravens and large raptors (Boarman and Heinrich 1999). Additionally, mobbing is a common behavior exhibited by ravens during spring months that align with sage-grouse lekking (Altmann 1956, Freeman and Miller 2018).

After inclement weather, ravens were one of the most common causes of disturbance to sage-grouse lek behavior. Previous evidence suggested that sage-grouse were tolerant to disturbance by ravens at specific lek sites (Bradbury et al. 1989), but our study is the first to quantify this antagonistic species interaction across a relatively broad landscape using extensive lek survey data. Evidence of ravens inducing changes in sage-grouse behavior on leks warrants increased consideration of ravens directly impacting sage-grouse reproductive success by potentially reducing breeding opportunities and driving variation in lek attendance and concomitant sources of error in lek surveys that index sage-grouse population trends (Connelly et al. 2003, Coates et al. 2021*b*).

We also found that ravens had similar probabilities of inducing sage-grouse flushing as golden eagles and coyotes, both predators of adult and yearling sage-grouse. This is concurrent with Dinkins et al. (2012), which reported that sage-grouse reacted similarly to ravens and other medium-sized birds in general, rather than identifying them by species. Thus, sage-grouse may view ravens as a similar threat comparable to known predators of adult and yearling sage-grouse. Although other studies have noted that golden eagle depredations of lekking sage-grouse were relatively rare (Hartzler 1974, Bradbury et al. 1989), we confirmed 3 successful attacks on lekking sage-grouse during our surveys. Though direct comparisons are difficult to make due to the nature of this analysis, our data is congruent with previous sources (e.g., Scott 1942, Hartzler 1974, and Ellis 1984) that observed high levels of flushing in the presence of golden eagles. Interestingly, raptors such as prairie falcons and northern harriers were less likely to induce behavioral changes in sage-grouse even though they are known to depredate adult and juvenile grouse

(Fletcher et al. 2003, Conover and Roberts 2017). Importantly, this could be a function of how frequently they occur in and around leks, with these species only observed during 1 and 6 lek counts, respectively. Inclement weather was a commonly observed reason for sage-grouse to not display, though it had relatively little effect on flushing behavior, indicating that species such as golden eagles, coyotes, and ravens presented a greater threat to sage-grouse than weather given the higher level of flushing.

We observed high probabilities of disturbance caused by ungulates, which is consistent with findings from Muñoz et al. (2021), wherein they found higher probabilities of grouse being absent from leks when non-native ungulates were present. Notably, our results are not directly comparable to Muñoz et al. (2021) as we did not investigate differences in native versus non-native ungulates, nor did we examine probabilities of sage-grouse lek attendance or typical displaying behavior in response to various disturbances.

There are important caveats and limitations within this study that should be recognized. For example, we lacked sufficient data to investigate multi-predator combinations (e.g., ravens and coyotes). Lek surveys with multiple causes of disturbance were considered unknown in the model to eliminate potential confounding of effects. Other sources of potential observational error were less controllable. Cryptic predators (e.g., coyotes) may have gone undetected by observers, which could lead to underestimation of sage-grouse disruptions by these predators. Similarly, instances of flushing by observers in the absence of predators may have led to overestimation of disturbance events. However, we removed observations where observers explicitly stated they were the direct cause for sage-grouse disturbance.

Additionally, counts of sage-grouse generally peak around sunrise and decline thereafter (Monroe et al. 2016), with most leks having dispersed within an hour (Jenni and Hartzler 1978) of sunrise. For example, using sunrise time (Time and Date AS 2021) from Battle Mountain, Nevada (the approximate geographical midpoint of our study), we found that approximately 89% of disturbances observed within this study occurred after sunrise and approximately 23% occurred an hour or more after sun-

rise. This indicates that at least some of these events are likely due to sage-grouse leaving the lek after sunrise, especially those without disturbance from animals or weather (Jenni and Hartzler 1978). Such behavior is expected (Jenni and Hartzler 1978) and is thought to decrease sage-grouse vulnerability to avian predators such as golden eagles (Hartzler 1974).

Finally, this was a post hoc study utilizing data collected for a larger study of sage-grouse population trends. Our study points to potential biases associated with lek surveys to estimate sage-grouse abundance, which has important implications for managers making informed decisions given the current focus on relating sage-grouse trends to patterns of surface land disturbance (Hagen 2011, Blomberg et al. 2013, Coates et al. 2021*b*). Substantial progress has been made describing abiotic factors influencing lek attendance and detectability once on lek (Monroe et al. 2016; Baumgardt et al. 2017; Fremgen et al. 2017, 2018; Coates et al. 2019; Wann et al. 2019). Only recently, however, have interspecific interactions at leks garnered attention as another source of variation (Muñoz et al. 2021), and our results add to this new body of knowledge that could help improve standardized lek survey protocols (e.g., Connelly et al. 2003) and estimation techniques (e.g., Coates et al. 2019). Importantly, failure to consider the presence of ravens (or other predators) could have especially strong consequence if leks are only counted once during a breeding season or in areas of high raven (or other predator) abundance. Hence, further study of these direct interactions between ravens and lekking sage-grouse are likely warranted and may elucidate previously unknown mechanisms driving patterns in sage-grouse abundance. Going forward, alternative remote monitoring techniques, such as video-recording, may provide improved estimates of predator impacts on sage-grouse behavior in the absence of human presence. Furthermore, a study design and collection procedures that directly study this question are necessary to reinforce the conclusions presented here.

Taken together, our study presents direct accounts of ravens attacking sage-grouse on leks, demonstrates changes in sage-grouse lek behaviors in response to ravens, and suggests that ravens are attracted to lek sites, indicating that ravens may have consequential impacts on

sage-grouse reproduction. These consequences are likely to be exacerbated by increases in raven abundance throughout western North America. Within the Great Basin ecoregion, raven population numbers were recently estimated to be 4.6 times greater than 53 years ago (Harju et al. 2021*b*). Although ravens are native to western North America, the proliferation of anthropogenic resource subsidies coupled with recent land cover modifications are thought to be the main drivers for increasing raven distribution and abundance (Kristan and Boarman 2007, Webb et al. 2011, O'Neil et al. 2018, Coates et al. 2020), which are similar to life history characteristics of invasive species (Carey et al. 2012). Golden eagle, coyote, and most raptor populations are typically not increasing at the same levels as ravens within the Great Basin (Bartel et al. 2008, Millsap et al. 2013, Sauer et al. 2017). Thus, while occurrence of these predators at sage-grouse leks is likely to maintain at current levels, disturbances by ravens are likely to increase. Hence, the disruptive potential of ravens at sage-grouse lek sites coupled with the effectiveness of ravens in depredating nests (Coates and Delehanty 2010, Howe and Coates 2015, Harju et al. 2021*a*) suggests that growing raven populations represent an increasingly complex and multifaceted threat to sage-grouse conservation efforts in the Great Basin.

### Management implications

Our observations of ravens during lek surveys and visual recordings suggest that they are disruptive to sage-grouse breeding behavior. Our study indicated that larger leks are more likely to be selected by ravens and are thus at a greater risk of these disruptions, as these leks are likely a focal point from which ravens hunt sage-grouse nests. Therefore, the cumulative impacts of ravens selecting sage-grouse lek sites, disruptions to sage-grouse breeding behavior, and reported impacts to nest survival have substantial implications to sage-grouse conservation, especially considering that raven population numbers are growing substantially in cold desert sagebrush ecosystems. Furthermore, lek disruptions by ravens and other predators identified in our study were a significant source of variation influencing lek attendance probabilities that should be considered in sage-grouse population models.



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## Supplemental materials

Supplemental material can be viewed at <https://digitalcommons.usu.edu/hwi/vol15/iss3/12>.

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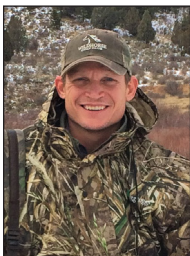
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Associate Editor: David K. Dahlgren

**JOSEPH L. ATKINSON** is a biological science technician who has worked with the U.S. Geological Survey since 2015. He received his B.S. degree in evolution, ecology, and biodiversity and a minor in avian sciences from the University of California, Davis. His research focuses on the ecology of western galliform birds and corvids, especially in the Great Basin.



**PETER S. COATES** is a research wildlife biologist for the U.S. Geological Survey, Western Ecological Research Center. He obtained a Ph.D. degree from Idaho State University and an M.S. degree from University of Nevada Reno. His research currently focuses on population ecology of greater sage-grouse and other sensitive prey species. Specifically, he investigates relationships between species' habitat, predators, and climate. His studies also focus on how anthropogenic-resource subsidies influence changes in raven and other predator populations. His research findings are intended to help inform management practices and guide resource policies using quantitative decision support tools.



**BRIANNE E. BRUSSEE** is a wildlife biologist for U.S. Geological Survey Western Ecological Research Center. She got her undergraduate degree from Ohio University in 2006 and completed a master's degree at University of California, Davis in 2013, where she studied black-crowned night-heron nest predation by ravens and nesting behavior using video-monitoring on Alcatraz Island.

Her current work focuses primarily on analysis of greater sage-grouse habitat and life-stage mapping as well as studies of raven abundance, density, and impacts to prey.

**MARK A. RICCA** is a research manager with U.S. Geological Survey (USGS) Forest and Rangeland Ecosystem Science Center. He has worked on applied research questions facing sagebrush ecosystems since 2014, much of which at USGS Western Ecological Research Center in the Coates lab.



**IAN A. DWIGHT** is an environmental scientist for the California Department of Fish and Wildlife, specializing in upland game research and management. He spent 9 years working for the U.S. Geological Survey Western Ecological Research Center and earned both his B.S. degree in wildlife, fisheries, and conservation biology and M.S. degree in avian sciences from the University of California, Davis. His current focus is developing population monitoring and management frameworks for game birds in California using a science-based approach.



**PAT J. JACKSON** graduated from the University of Missouri in 2007 with a bachelor's degree in forestry and another bachelor's degree in fisheries and wildlife. After graduation, he enjoyed a short stint of wildlife field work in southeast Alaska, transitioned to full-time trapping in Missouri, and then moved to



Hawaii in 2008. In Hawaii, he spent 2 years doing vertebrate pest work focusing on feral cats, rats, and feral swine removal. In 2010, he moved to Utah and began work on a Ph.D. degree focusing on coyote biology, diet, and home ranges in central Nevada. He is currently the predator management staff specialist for Nevada Department of Wildlife. His professional interests include wildlife damage management, animal capture techniques, best management practices for furbearer trapping, public outreach, and predator management. He is an avid trapper, fisherman, and hunter, primarily focusing on big game in the west. One of his favorite aspects involves teaching others to big game hunt and trap. He also thoroughly enjoys sharing and teaching others to butcher and prepare wild game.