

Inter- and intra-annual effects of lethal removal on common raven abundance in Nevada and California, USA

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Abstract: Populations of common ravens (*Corvus corax*; ravens) have increased rapidly within sagebrush (*Artemisia* spp.) ecosystems between 1960 and 2020. Although ravens are native to North America, their population densities have expanded to levels that negatively influence the population dynamics of other wildlife species of conservation concern, such as greater sage-grouse (*Centrocercus urophasianus*) and desert tortoises (*Gopherus agassizii*). For this reason, lethal removal, such as the application of the avicide DRC-1339, has been used to manage raven numbers at local scales and under certain circumstances. Because the relative effectiveness of DRC-1339 in reducing raven population densities is not thoroughly understood, we completed 2 case studies using a before-after-control-impact experimental design of density estimates generated from point count data within a Bayesian hierarchical distance sampling framework. Specifically, we analyzed >16,000 point count surveys collected during 2009–2019 and split into 2 study designs covering multiple field sites within the Great Basin region. The first experiment evaluated intra-annual changes in density by comparing before and after treatment time periods within a single breeding season for multiple treatment regions compared to 2 control regions. The other experiment focused on inter-annual differences by comparing time periods across years before and after the onset of annual avicide application for a single treatment region compared to multiple control regions. Our models estimated a 100% probability of decline in density relative to control sites for both the intra- and inter-annual model designs. At treatment sites, expected densities of ravens varied but were reduced by 43% (95% CRI: 33–49%) and 54% (95% CRI: 24–71%) according to intra- and inter-annual analyses, respectively, whereas densities increased by 42% (95% CRI: 27–60%) and 15% (95% CRI: -17 to 58%) at control sites. Although population densities were reduced with treatments, trends indicated that sustained effort would likely be needed to maintain densities at acceptable levels within regions of interest. Effectively reducing the adverse effects of raven populations on other native species likely will depend on a variety of targeted management actions such as improving habitat quality for prey species, possibly reducing ravens' population density, and treating the cause of increased raven abundance to reduce future carrying capacity and prevent rebounds.

Key words: avicide, *Centrocercus urophasianus*, common raven, *Corvus corax*, distance sampling, DRC-1339, greater sage-grouse, hierarchical distance sampling, lethal removal, nest predators, point count

COMMON RAVENS (*Corvus corax*; ravens) are large, omnivorous passerine birds with wide geographic distributions. Ravens are native to North America and have dramatically increased in abundance while expanding in distribution between the 1960s and present day (Boarman 1993, 2003, Sauer et al. 2017). Consequently,

scientific evidence has accumulated regarding the implications of elevated raven populations for lower trophic level species (Boarman 1993, Coates et al. 2020). Ravens opportunistically forage on a wide breadth of food items, allowing them to benefit from anthropogenic food sources that subsidize natural sources in en-

vironments that might otherwise have limited resource availability (Kristan et al. 2004, Bui et al. 2010, Coates et al. 2016a). In addition, ravens can be adept visual predators, targeting nests and vulnerable juveniles as prey (Boarman 2003, Coates et al. 2008, Shields et al. 2019).

Ravens can exhibit elevated and sustained predation rates on prey species, in part due to resource subsidization, which may have detrimental effects to these populations (Boarman 2003, Berry et al. 2020, Coates et al. 2020). The impacts of ravens have been particularly well-documented in relation to greater sage-grouse (*Centrocercus urophasianus*) and desert tortoise (*Gopherus agassizii*) populations by way of reduced nest success (Coates and Delehanty 2010, Dinkins et al. 2016, Coates et al. 2020) and juvenile survival (Boarman 2003, Kristan and Boarman 2003), but similar impacts likely extend to other species as well (Colwell et al. 2005, Peery and Henry 2010, Ellis et al. 2020). Observations of widespread impacts on sensitive prey species have raised concerns among wildlife biologists and managers that continued growth of raven populations will correspond with declines in abundance and suppression of recovery for several species of conservation concern.

Ravens are protected under the Migratory Bird Treaty Act (16 U.S.C. §§703–712; MBTA), so preferred management options for the species primarily involve nonlethal methods. However, the effectiveness of nonlethal methods can be variable (Avery et al. 1995, Merrell 2012, Peterson and Colwell 2014, Scasta et al. 2017), and these options may not be feasible on their own when management objectives involve reducing raven densities to relieve predation pressure affecting species of conservation concern. Consequently, lethal removal is sometimes deemed necessary through special authorization from the U.S. Fish and Wildlife Service and has commonly involved application of the compound CPTH (3-chloro-p-toluidine hydrochloride), or DRC-1339 (U.S. Department of Agriculture [USDA] 2019), which is considered a legal toxicant for raven control by the U.S. Environmental Protection Agency (Spencer 2002, Coates et al. 2007). Application of DRC-1339 typically involves treatment of an attractive food source such as poultry eggs or dog (*Canis familiaris*) food and distribution of the treated bait to high use areas such as landfills, roadkill, or carcasses

(Coates et al. 2007, Peebles and Conover 2016), which are then consumed by ravens.

Lethal raven removal using DRC-1339 has had measurable effects when previously studied at small spatial scales and time lags (1–2 years following application), resulting in estimated reductions in local raven populations over relatively short time periods. For example, raven numbers declined at treated sites while remaining stable or increasing at untreated sites during 2002–2005 in Nevada, USA (Coates et al. 2007), and 2008–2011 in Wyoming, USA (Dinkins et al. 2016). In addition, population declines of 9–12% were observed over 2 years corresponding to removal of 7–34% of the treated population in a Wyoming study during the winters of 2014–2015 (Peebles and Conover 2016).

In some cases, positive responses in prey species demographics have been detected in locations where raven removal efforts were prevalent. For example, sage-grouse nest success can vary in relation to local raven abundance (Coates and Delehanty 2010, Dinkins et al. 2016, Coates et al. 2020), and removing ravens can increase nest success (Dinkins et al. 2016) and possibly lead to population-level influences (Peebles et al. 2017), though improvements in sage-grouse population numbers have not been consistent (Conover and Roberts 2017). However, raven populations appear to rebound rapidly (≥ 1 year) following termination of removal efforts (Peebles and Conover 2016), and the relative effectiveness and potential limitations of DRC-1339 treatments are not well understood, in part because of the difficulty and resources involved in performing reliable and comparative estimation of raven population abundances at relevant spatial scales where DRC-1339 was applied relative to control areas (i.e., no treatment). Further, raven population densities may exhibit high spatial and temporal variance in response to environmental conditions, so standardized monitoring approaches that span multiple years at treated and untreated sites are likely needed to accurately quantify removal effects.

Our objective in this study was to evaluate the effectiveness of raven removal by corvidicide treatment, both within the breeding season time frame (i.e., intra-annual) and across time with continued annual treatment applications (i.e., inter-annual). The purpose of treatment within both time frames was to reduce raven

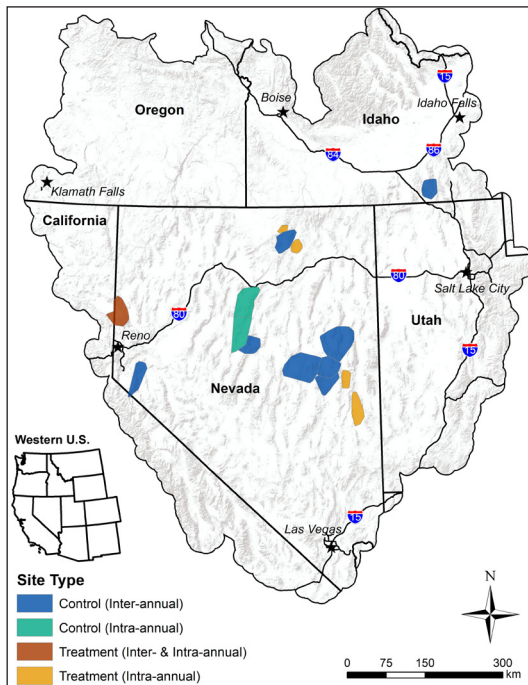


Figure 1. Locations of field sites in Nevada and California, USA, 2009–2019, where densities of common ravens (*Corvus corax*) were evaluated under a before-after-control-impact study design within years (intra-annual) and across years (inter-annual), where treatment sites were associated with the application of the avicide DRC-1339. Sites were color coded according to time period (inter- vs. inter-annual) and treatment vs. control.

density, as previous research has indicated the potential for reduced densities to alleviate predation pressure on sensitive prey species (Dinkins et al. 2016, Peebles et al. 2017, Coates et al. 2020). For both case study time frames, we approached the problem by estimating raven abundance from point count survey data at 1 or more study sites where avicide treatments were completed (i.e., treatment sites) and contrasting the counts to 1 or more “control” sites where treatments did not occur.

To account for the possible confounding influences of random or systematic differences among and between treatment and control sites, we evaluated the counts using a before-after-control-impact (BACI) study design (Eberhardt 1976), which isolates and allows quantification of the true treatment influence under these circumstances. Scientific knowledge about the effectiveness of these treatments on different time scales advances the capacity of wildlife managers to implement adaptive management actions

in situations where lethal raven removal is an acceptable strategy for reducing raven impacts on prey species.

Study area

We completed our study during the breeding seasons of 2009–2019 at multiple field sites within Nevada, 1 field site that occurred in northeastern California, USA and bordered northwestern Nevada, and 1 field site in southeastern Idaho, USA (Figure 1). Study sites were split into those monitored by the Nevada Department of Wildlife (NDOW) for the primary purpose of investigating raven densities and effectiveness of removal ($n = 7$), and those that were monitored by U.S. Geological Survey (USGS; $n = 9$) as part of an ongoing study of sage-grouse population dynamics in the Great Basin region.

All study sites were characteristic of Great Basin sagebrush (*Artemisia* spp.) ecosystems, comprising high elevation, temperate cold desert environments. Shrubs were interspersed with grasses, forbs, and coniferous forest at moderate-to-high elevations with intermittent dry or saline lake beds occurring at the lowest elevations. Shrub species included sagebrush, rabbitbrush (*Chrysothamnus* spp.), horsebrush (*Tetradymia* spp.), greasewood (*Sarcobatus* spp.), common snowberry (*Symphoricarpos* spp.), serviceberry (*Amelanchier* spp.), fourwing saltbrush (*Atriplex* spp.), and bitterbrush (*Purshi* spp.). Common herbaceous species included wheatgrass (*Agropyron* spp.), fescue (*Festuca* spp.), bluegrass (*Poa* spp.), needlegrass (*Stipa* spp.), brome grass (*Bromus* spp.), and squirrel-tail (*Sitanion* spp.). Vegetation type depended on variation in precipitation, temperature, soil, topographic characteristics, and elevation (Miller et al. 2011).

The primary land use was rangeland with interspersed irrigated or dry cropland agriculture. The density of human development was relatively low throughout the remote, mountainous landscape, and most typically was characterized by roads, power lines, and distribution lines associated with agricultural communities. Oil, gas, and geothermal energy developments were present, and mine sites were common throughout the region. We provide summaries of landscape characteristics occurring within each site boundary in Appendix Table S1.

Methods

Data collection

At all study sites and years, we conducted point count surveys for ravens to estimate density before and after treatments within a year (intra-annual design) and across years (inter-annual design). All surveys for both designs consisted of a 10-minute point count occurring between 30 minutes after sunrise to 30 minutes before sunset. Surveys were completed throughout the day to maximize effort and sample size while ravens were active. Observers recorded all ravens observed within a 2.5-km radius with binoculars and by unassisted vision, including the group size (≥ 1), time of observation, horizontal distance to group or individual (m), bearing ($^{\circ}$) to the center of the group or individual, and behavior at first detection. Rangefinders, hand-held global positioning system transmitters (Garmin, Garmin International Inc., Olathe, Kansas, USA), and compass were used to estimate distance and bearing. We did not perform surveys under poor weather conditions, such as fog, rain, or excessive wind (Walker and Marzluff 2015, Coates et al. 2020). We used all group size observations to comprehensively estimate density of all types of ravens (i.e., resident pairs, transient groups), because inferring status by group size and behavior would have been confounded by imperfect detection and potentially subjective assignments by observers.

For the intra-annual design, we surveyed random locations across 6 treatment study sites and 2 control sites (Figure 1) during March to August each year, 2017–2019. Daily surveys were separated by at least 2.5 km, and all surveys were separated by at least 1 hour or 5 km to minimize spatiotemporal dependence among surveys (Walker and Marzluff 2015). These distances were chosen based on estimates of raven movement patterns (< 1 km/hour for breeding ravens, 2.8 km/hour for non-breeding ravens; Harju et al. 2018). We surveyed 50–85 locations at each study site visited each year; due to agency resources, surveys were conducted at 5, 7, and 5 sites during 2017, 2018, and 2019, respectively. To survey an adequate number of sites for modeling, approximately 70% of all survey locations occurred within 500 m of a road, 20% were 500–1,000 m from a road, and 10% were > 1 km from a road. Otherwise, sur-

veys were not stratified by land cover type. The control sites were surveyed every year to facilitate BACI comparisons. We prioritized survey effort across treatment and control sites to ensure that a minimum of 60 observations were gathered per strata to meet established recommendations for distance sampling analysis (Buckland et al. 2001). We visited each survey location twice each year to establish a paired design, once before treatments were applied (March 1 to May 7) and once afterward (June 1 to August 7).

For the inter-annual design, we conducted surveys at 9 study sites (Figure 1) that were part of a long-term monitoring data collection program beginning in 2009. Avicide treatments were initiated at 1 of these study sites in 2014 (Figure 1) and continued each of the following years (2015–2019). The remaining sites ($n = 8$) were used as controls and were selected because the timing of data collection spanned years prior to and after the initiation of raven removal at the treatment site. At all sites, raven point count surveys were conducted at locations where sage-grouse data were collected and at independent random locations each year between March and August. Survey effort at control sites varied from year to year, but collective observations at control and treatment sites easily exceeded the 60 observation minimum recommendation (Buckland et al. 2001).

DRC-1339 treatment

The USDA, Animal and Plant Health Inspection Service (APHIS), Wildlife Services (WS) distributed DRC-1339-treated bait annually at treatment field sites each year between March and May (depredation permit: U.S. Fish and Wildlife Service MB37116A-0). Wildlife Services partnered with NDOW to select and monitor field sites for the intra-annual study, while the USGS continuously monitored raven abundance at the treatment site for the inter-annual design (Lockyer et al. 2013). For the inter-annual study design, we evaluated long-term population reduction as a primary objective. Therefore, application occurred annually, and point count surveys were initiated at the onset of treatment and carried out through the treatment period.

However, for the intra-annual study design, we conducted point count surveys pre- and

post-treatment within the same year because the primary objective was to estimate immediate reduction in raven density within a year. Application of DRC-1339 followed procedures outlined in Peebles and Spencer (2020). Specifically, WS treated eggs using a 97% active ingredient powder mix with potable water into egg baits (e.g., hard-boiled chicken [*Gallus gallus domesticus*] eggs), which were then placed in locations that had been pre-baited and exhibited high activity for the target species only (Peebles and Spencer 2020). Pre-baiting with non-toxic baits were placed at proposed sites prior to the application of treated egg baits to determine whether non-target species occurred in the treatment area and would be likely to consume bait (Peebles and Spencer 2020). Treatment sites were then avoided if non-target species were present and subsequently monitored by personnel to prevent consumption by non-target species (Coates et al. 2007, Peebles and Spencer 2020).

For the inter-annual study, an average of 86 g (SD = 31) and 4,291 eggs (SD = 1,543) were deployed annually at the treatment site. The treatment sites for the intra-annual study ranged from 4–86 g and 200–4,290 eggs deployed annually per site, with annual averages of 36 g (SD = 13) and 1,793 eggs (SD = 649) across all treated sites. Methods of egg deployments were comparable at the treatment sites for both the intra- and inter-annual study design.

Data analysis

We estimated raven abundance and densities at all survey locations using distance sampling methods (Buckland et al. 2001, Schmidt et al. 2012, Sillett et al. 2012). In our intra-annual analysis, we specified models to estimate abundance at each site and survey location before and after treatment was implemented within each year. In our inter-annual analysis, our sites were split into before and after treatment across years (before = 2009–2013; after = 2014–2019).

We used a Bayesian hierarchical model to estimate declining probability of detection as distance from observer increased (i.e., distance sampling) and thus infer estimates of true abundance within a known survey area, which facilitates calculations of density (Buckland et al. 2001, Thomas et al. 2010, Kéry and Royle 2015). We modeled the unknown latent abundance (n_{jpr}) at each survey ($p = 1, \dots, P$) within each site

($j = 1, \dots, J$), during each year ($r = 1, \dots, R$), after conditioning on detection probabilities. We followed methods described by Oedekoven et al. (2014) and used an integrated likelihood,

$$L_{n,y}(\boldsymbol{\beta}, \boldsymbol{\theta}) = L_n(\boldsymbol{\theta})L_n(\boldsymbol{\beta} | \boldsymbol{\theta}) \quad (1)$$

where ($L_y(\theta)$) is the detection likelihood and ($L_n(\beta | \theta)$) is the observed count likelihood.

The likelihood component for detection ($L_y(\theta)$) is a function of distance from the observer, the expected distribution of animals with respect to the observer, the truncation distance (Thomas et al. 2010), and probability of detection, including any specified covariates. We included observations within 1.2 km from the observer, the approximate distance at which detection probability decayed to <0.1 (Buckland et al. 2001). To model probability of detection, we used a half-normal detection function (Thomas et al. 2010, Oedekoven et al. 2014, Kéry and Royle 2015):

$$g(y | \theta) = \exp\left(\frac{-y^2}{2\sigma^2}\right) \quad (2)$$

where y represented distance to the observed group of ravens and σ^2 represents the scale parameter. We incorporate landscape influences on probability of detection, we modeled σ as a function of environmental covariates (α ; Marques et al. 2007, Oedekoven et al. 2014) representing area of viewshed and percent forested area within the 1.2-km radial buffer surrounding the observer. These covariates were calculated for each survey location using visibility analysis and zonal statistics tools by way of ArcPy (ArcMap 10.5; Environmental Systems Research Institute [ESRI], Redlands, California) for Python 2.7 (Python Software Foundation, <http://www.python.org>). Further details regarding the geospatial analysis are available in Coates et al. (2020).

The likelihood component for observed counts ($L_n(\beta | \theta)$) is Poisson-distributed with an intensity parameter λ_{jpr} , where $E(n_{jpr}) = \lambda_{jpr}$. Within the model for observed counts, we also included site-year as a random effect and factor covariates for control group (i.e., control vs. treatment) and time period (i.e., before vs. after). To make inference on the effects of DRC-1339 treatment, we compared the estimated density of ravens in each control group (i.e.,

control vs. treatment) and time period (i.e., before vs. after), where density, D_{jpr} , was calculated at each survey location,

$$D_{jpr} = \lambda_{jpr} / v(\theta) \tag{3}$$

with effective area of the survey $v(\theta) = 2\pi \int_0^w y g(y|\theta) dy$. We then averaged the survey densities for each site-year in the inter-annual analysis and for each time period (before, after treatment) within each site-year in the intra-annual analysis. The expected number of ravens for surveys in each control group and time period was obtained by

$$N_l = \frac{1}{J_l} \sum_{j=1}^{J_l} \frac{1}{P_l} \sum_{p=1}^{P_l} \frac{1}{R_l} \sum_{r=1}^{R_l} \lambda_{jpr} \tag{4}$$

for $l = BC, AC, BT, AT$ indicating before-control, after-control, before-treatment, and after-treatment BACI categories, respectively. As such, the BACI ratio estimates the effects for both the intra- and inter-annual design using the abundances within our survey sites across each category. We quantified the overall treatment effect by calculating the posterior distribution of the BACI ratio (Conner et al. 2016):

$$R_{BACI} = \frac{N_{AT} / N_{AC}}{N_{BT} / N_{BC}} \tag{5}$$

By deriving the posterior distribution of the BACI ratio, we provide probabilistic interpretation of the treatment effect while accounting for temporal environmental stochasticity, where an R_{BACI} value < 1 would imply lower abundance (λ_{jpr}) in treatment groups relative to controls after treatments occurred.

We developed a custom Markov chain Monte Carlo (MCMC) algorithm in R Statistical Software (R Development Core Team 2021) to estimate the posterior distributions of the unknown parameters, given the data. We first simulated data under biologically appropriate parameters and verified that the MCMC sampler recovered the true parameters (Little 2006). We then fit the model to the observed data, obtaining 100,000 draws from the posterior distribution using our MCMC and discarding the first 50,000 to permit tuning and convergence from arbitrary starting values. We thinned the posterior samples by retaining every tenth sample, resulting in 5,000 samples used for

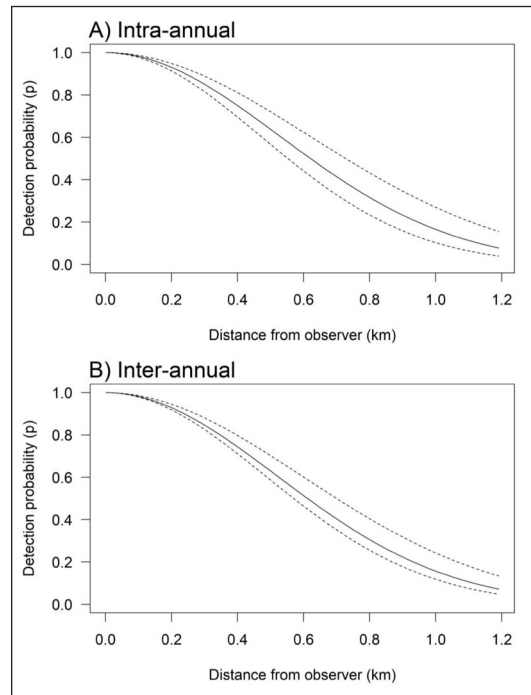


Figure 2. Relationship between probability of detecting common ravens (*Corvus corax*; ravens) and distance from observer and 95% credible intervals, as informed by Bayesian hierarchical distance sampling of raven point count survey data collected in Nevada and California, USA, 2009–2019. Two separate models were fit to data at separate study areas following (A) a study design where densities were estimated before and after raven removal was conducted within the same year (intra-annual, years 2017–2019), and (B) a study design investigating densities annually (inter-annual, 2009–2019), before and after raven removal was initiated at a treatment site starting in 2014.

inference. We evaluated convergence from visual examination of traceplots and verification of \hat{R} values < 1.01 (Gelman et al. 2013). We calculated the median and 95% credible intervals from posterior distributions of all parameters, including R_{BACI} . The model’s effects were interpreted as the treatment influences on the number of ravens per our survey area (ravens km^{-2}).

Results

We observed 3,832 ravens at 2,600 unique surveys over 3 years within the 7 field sites where the intra-annual study design was implemented. Likewise, we observed 6,378 ravens at 13,294 unique surveys over 11 years within the 9 field sites where the inter-annual study design was implemented. Observation rates (i.e., number of ravens per point count survey)

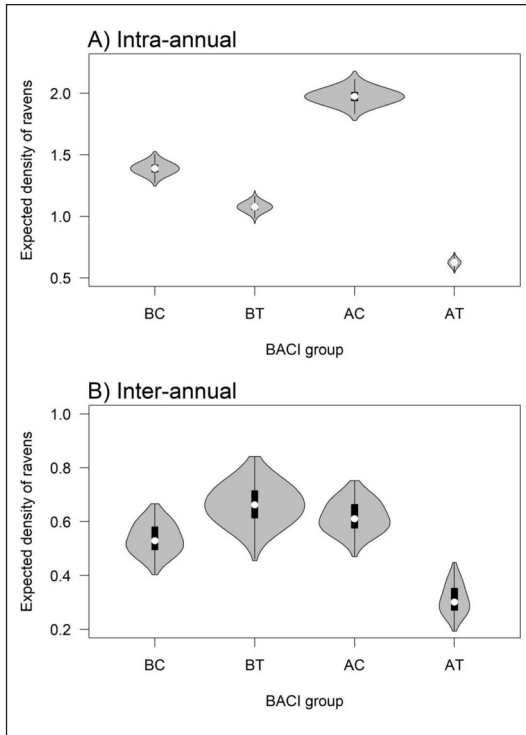


Figure 3. Estimates of average common raven (*Corvus corax*; raven) densities (ravens km⁻²) from raven point count surveys conducted in Nevada and California, USA, 2009–2019, and evaluated using Bayesian hierarchical distance sampling. Raven densities were contrasted across before-after-control-impact categories, where treatment sites were associated with the application of the avicide DRC-1339 within the same year (A) and across years (B). Violin plots represent the posterior distribution of density estimates, where the open circle indicates the median estimate, the thick line indicates the interquartile range, the thin line indicates the 95% credible interval, and the shaded area indicates the kernel density of the probability distribution to show distributional shape of the posterior estimates.

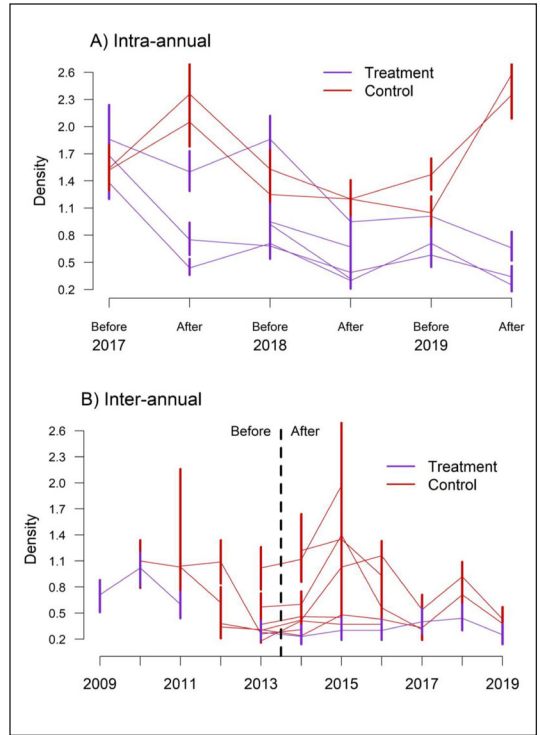


Figure 4. Mean annual densities of common ravens (*Corvus corax*; ravens) over 2 time series in Nevada and California, USA, 2009–2019. Raven densities were contrasted across before-after-control-impact categories, where treatment sites (purple lines) were associated with the application of the avicide DRC-1339 (A) within the same year (intra-annual study; 2017–2019) and (B) across years, 2009–2019, with treatment beginning in 2014 (inter-annual study; dashed line representing assignment to before/after group). Control sites were represented by red lines. Densities were estimated using Bayesian hierarchical distance sampling applied to point count survey data.

declined at surveys following treatments for both the inter- and intra-annual study designs (Appendix Table S2), but this was not the case for surveys occurring at control sites without raven avicide treatments.

Model for intra-annual design

Our model for intra-annual analysis of raven treatments converged with $\hat{R} < 1.01$ for all parameters. Probability of detection declined with distance to observer and averaged ~0.55 (Figure 2A). Detection probability was influenced negatively by percent forested area ($\alpha_1 = -0.041$, 95% CRI: -0.081 to 0.004) and positively by greater viewshed area ($\alpha_2 = 0.128$, 95% CRI:

0.076–0.181). We derived posterior distributions of expected raven abundance and density at surveys prior to and after avicide treatments (Appendix Table S2).

Expected raven densities increased from 1.39 (95% CRI: 1.30–1.47) ravens km⁻² to 1.97 (95% CRI: 1.87–2.08) ravens km⁻² in our control group. Although raven densities increased in control sites, raven densities decreased within treatment sites. Pre-treatment densities at treatment sites averaged 1.08 (95% CRI: 1.01–1.14) ravens km⁻². Post-treatment densities at treatment sites averaged 0.62 (95% CRI: 0.58–0.67) ravens km⁻² (Appendix Table S2; Figure 3A). Over the course of 3 years of application, model

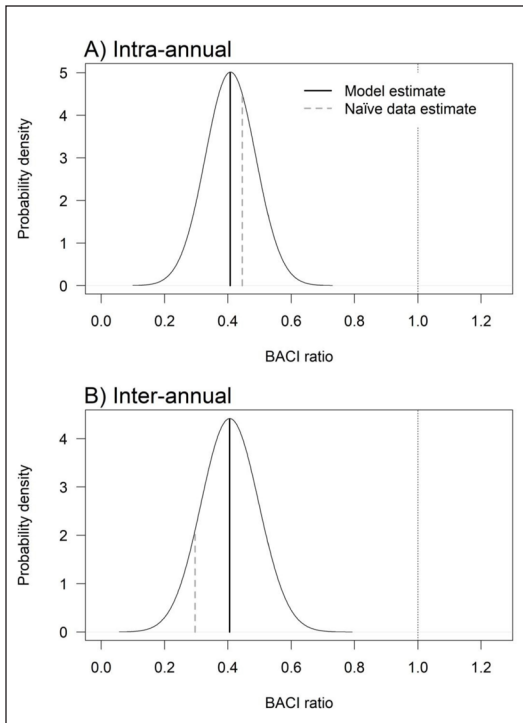


Figure 5. Ratios of average common raven (*Corvus corax*) densities in Nevada and California, USA, according to a before-after-control-impact (BACI) design, where treatment sites were associated with the application of the avicide DRC-1339 within the same year (A) and across years (B). The BACI ratio quantifies the change in densities at control sites (numerator) relative to changes in treatment sites (denominator) across a common time period, where a ratio value < 1 would imply lower densities in treatment groups relative to controls after treatments occurred.

derived densities at control sites remained relatively stable or increasing (Figure 4A). Before treatment at control sites, raven densities were 1.53 (95% CRI: 1.30–1.78) in 2017 and 1.26 (95% CRI: 1.10–1.44) in 2019. After treatments at control sites, raven densities were 2.21 (95% CRI: 1.92–2.55) in 2017 and 2.47 (95% CRI: 2.22–2.74) ravens km^{-2} in 2019, respectively. In contrast, at treatment sites, raven densities declined over time (Figures 3A and 4A). Densities before treatment were 1.64 (95% CRI: 1.32–2.02) in 2017 and 0.77 (95% CRI: 0.63–0.93) in 2019. After treatments, raven densities at treatment sites were 0.90 (95% CRI: 0.74–1.07) in 2017 and 0.42 (95% CRI: 0.32–0.55) ravens km^{-2} in 2019, respectively.

Our model results suggested the observed declines in raven density could be attributed to avicide treatments based on combined effects of

treatment site versus control sites. Collectively, these results corresponded to a modeled BACI ratio of 0.41 (95% CRI: 0.36–0.46) reflecting the 42% increase on average at control sites (95% CRI: 27–60%) as opposed to a 43% decrease on average at treatment sites (95% CRI: 33–49%). Our results also indicated a 100% probability of a decline in raven abundance at treatment sites relative to the controls, as the posterior distribution of the BACI ratio did not overlap 1.0 (Figure 5A).

Model for inter-annual analysis

The model for inter-annual analysis converged with $\hat{R} < 1.01$ for all parameters. Probability of detection declined with distance to observer and averaged ~ 0.54 (Figure 2B). Detection probability was not strongly influenced by percent forested area ($\alpha_1 = -0.01$, 95% CRI: -0.04 to 0.01) and was positively influenced by greater viewshed area ($\alpha_2 = 0.11$, 95% CRI: 0.06–0.15). As in our intra-annual analysis, we derived posterior distributions of raven abundance and density at surveys prior to and after avicide treatments (Appendix Table S2).

Expected raven densities increased from 0.53 (95% CRI: 0.45–0.63) ravens km^{-2} to 0.61 (95% CRI: 0.52–0.71) ravens km^{-2} during the time periods of 2009–2013 (pre-treatment) and 2014–2019 (post-treatment) at our control sites. Again, as raven densities increased in control sites, raven densities decreased in treatment sites when comparing the same time periods. Pre-treatment densities at treatment sites were 0.66 (95% CRI: 0.54–0.78) ravens km^{-2} . Post treatment densities at treatment sites were 0.30 (95% CRI: 0.23–0.41) ravens km^{-2} (Appendix Table S2; Figures 3B and 4B). These results again suggested an effect of the avicide treatment based on combined effects of treatment site versus control sites. Collectively, results corresponded to a modeled BACI ratio of 0.40 (95% CRI: 0.32–0.50) reflecting the 15% increase on average at control sites (95% CRI: -17 to 58%) as opposed to a 54% decrease on average at treatment sites (95% CRI: 24–71%). These results additionally indicated a 100% probability of a decline in raven abundance at treatment sites relative to the controls, as the posterior distribution of the BACI ratio did not overlap 1.0 (Figure 5B).

Discussion

This study quantified the relative effectiveness of a commonly used strategy, the application of

DRC-1339, to lethally reduce raven densities at study sites within southwestern sagebrush ecosystems in the United States (Larsen and Dietrich 1970, Spencer 2002, Coates et al. 2007, Peebles and Conover 2016). We observed evidence that application can be effective in reducing localized raven abundance, and this study was the first to quantify immediate reduction in population numbers (intra-annual) and investigate potential for sustained reduction over multiple years of application (inter-annual) at separate field sites. In both time frames, raven abundances were lower at 1 or more treated sites relative to 1 or more untreated sites. Although we could not conclusively determine that reduced abundances were solely due to lethal effects, as opposed to movement away from the sites, our results generally align with other studies that quantified lethal take and showed reductions of raven abundance following treatment (Dinkins et al. 2016, Peebles and Conover 2016, Peebles et al. 2017). These results also indicate that the capacity for raven population increases continued to exist in our study region, as field sites where avicide treatments did not occur during the same time period experienced evidence of population increases.

While the results of our models demonstrated strong statistical evidence of reductions in raven densities following lethal removal efforts, relative to controls, our study had several important limitations. First, data were not available regarding precise coordinates of egg deployment along with actual estimates of the number of ravens killed across each treatment site and year combination. Thus, for each site-year combination, our models only account for whether or not raven lethal removal took place, and therefore only provide general, relative inference about the effort necessary to produce the modeled effect. For example, there was substantial variation in the number of eggs deployed (and associated weight of active ingredient) across both space (among sites) and time (among years).

Overall take could not be estimated in part due to the logistical difficulty of accurately detecting and collecting raven carcasses (Peebles and Conover 2016, Peebles and Spencer 2020). Because DRC-1339 acts slowly, death may not occur for 1–3 days following ingestion, and ravens usually leave the treatment area during this time (Spencer 2002). This renders collection

of carcasses difficult to impossible in rugged and remote terrain without use of transmitters or marked birds to facilitate retrieval (Conover and Roberts 2017). Because relative effort was not quantified, variation in the treatment effect was averaged across sites and years in our model, and we could not inform the specific level and cost of effort that would be needed in the future to produce the observed negative response in abundance. We consider this problem an important area for future research regarding lethal removal of common ravens.

A second limitation was that we were unable to collect or report data on consumption of DRC-1339 eggs by non-target species in this study, which can further complicate estimation of take by ravens because the rates of non-target species consumption are unknown (Coates et al. 2007). Such information is difficult to obtain without video or camera monitoring. Previous studies have indicated that consumption of egg baits by non-target species may occur at higher rates than expected, although the species identified were not expected to be at risk of fatality from baits or from scavenging of dead ravens (Spencer 2002, Coates 2006, Coates et al. 2007, Peebles and Spencer 2020). For example, in a previous study, the most common non-target species that consumed eggs were ground squirrels (*Spermophilus elegans*, *S. mollis*), and the concentration of DRC-1339 resulting in raven fatality ($LD_{50} = 5.6$ mg/kg) is ~180 times less than that of rodents similar sized or smaller than ground squirrels ($LD_{50} = 2,000$ and $1,170$ – $1,770$ mg/kg for mouse (*Mus musculus*) and white rat (*Rattus norvegicus*), respectively; Clark 1986, Coates et al. 2007). Further, the active ingredient in DRC-1339 decomposes rapidly and is generally expelled prior to death in ravens, thus limiting the risk of secondary poisoning (Spencer 2002).

Established protocols were followed to minimize exposure of non-target species to baits (Spencer 2002, Peebles and Spencer 2020), and egg baits were used to target ravens relative to other species that might be harmed by DRC-1339 based on LD_{50} (American crow [*C. brachyrhynchos*], red-winged blackbird [*Agelaius phoeniceus*], mourning dove [*Zenaidura macroura*], American magpie [*Pica hudsonia*]; DeCino et al. 1966, Coates 2006). Nonetheless, consumption of baits by non-target species warrants further investigation to assure that other species are largely unaf-

ected while also improving estimation of lethal take by accounting for total eggs missing. If research were to indicate that non-target species are impacted by DRC-1339, then the objective of reducing raven density using lethal techniques may be complicated by the risk of potential adverse impacts to other wildlife.

Our study investigated trends in raven abundance at geographically distinct regions following removal (i.e., treatment sites), and compared them to trends at regions where no removal occurred (i.e., control sites). Despite the large number of surveys conducted overall, we were unable to replicate treatment sites for the inter-annual design, and conversely could not replicate multiple control sites for the intra-annual design. During the early years of this study (inter-annual design), widespread use of raven removal was not considered viable and the treatment site was experimental. During later years, the intra-annual design was set up to further investigate lethal removal over the course of a single season as well as longer periods of time. However, resources and logistical constraints precluded visiting a larger number of sites, and treatment sites were prioritized above control sites. Because treatment sites were not replicated for the inter-annual design, and control sites were not replicated beyond 2 sites for the intra-annual design, it is possible that our results reflected localized trends. BACI effects may not transfer across additional control or treatment zones driven by other environmental factors, thus increasing the chance of Type I error according to our study design. Although we encourage further investigation, careful consideration should be taken when replicating treatment sites due to the potential for increased costs and undesired side effects of lethal removal.

Understanding the relationship between common raven population densities and prey species of concern can be useful when determining whether densities exceed levels that negatively affect these species or if management strategies have been effective in reducing populations to such levels. For example, implementing lethal raven removal may require strong justification, and demonstration of its effectiveness may be most meaningful in this context. To establish objectives in relation to population management of common ravens, the impacts to other

species can be quantified.

Other research in the Great Basin region has indicated that raven impacts to greater sage-grouse nest success are most evident when raven densities exceed ~ 0.40 ravens km^2 (Dinkins et al. 2016, Coates et al. 2020). Relative to this value, in our study, raven removal efforts were successful in reducing and maintaining raven density below this potential threshold over a long period of time (6 years, inter-annual design), though densities on average still exceeded 0.40 ravens km^2 over shorter periods of time despite being reduced every year (3 years, intra-annual design). Thus, for the purpose of managing raven abundance to benefit sage-grouse nest success, it is likely that multiple years of application are needed to reach densities below those previously identified as problematic for sage-grouse. Control sites in our study exhibited population increase across both time periods, exemplifying a common challenge for management of populations in systems such as the Great Basin where raven densities commonly exceed levels that negatively affect sensitive species such as sage-grouse (Coates et al. 2020).

While anthropogenic resource availability and nesting habitat continue to subsidize raven populations, raven removal efficacy will continue to be limited by the magnitude of raven population increases and will likely be best directed to specific problem areas in a sustained manner to prevent population rebound. Despite effectiveness in years of application, raven populations are likely to rebound in areas where treatments no longer occur, as has been indicated in other research (Coates et al. 2007, Peebles and Conover 2016, Conover and Roberts 2017). Because of these challenges, to prevent recolonization following treatments, long-term solutions will likely require alternative and additional management actions that focus on localized sources of raven population increases.

Management actions that focus on predator populations are unlikely to reverse population losses among sensitive species if other factors that limit these populations are not also addressed. For example, habitat loss and degradation has been detrimental to sage-grouse populations spanning multiple decades (Connelly and Braun 1997, Braun 1998, Schroeder et al. 2004, Aldridge et al. 2008) due to factors

such as land cover change (Braun 1998), anthropogenic and energy development (Walker et al. 2007), encroachment of coniferous tree cover (Baruch-Mordo et al. 2013, Severson et al. 2017), and changing climate and wildfire regimes (Coates et al. 2016b). In desert tortoise populations, while predation of juveniles by ravens has been implicated as a key factor suppressing desert tortoise populations (Boarman 1993), other drivers may include severe drought, habitat conversion, disease, and invasion by non-native species (Peterson 1994, Esque et al. 2010, Averill-Murray et al. 2012). These multiple factors may interact with predator densities to affect either species (i.e., greater sage-grouse, desert tortoise) because raven predation rates and relative influences on prey are likely dependent on variation in habitat conditions. For example, the influence of raven abundance on sage-grouse nest success was shown to be a function of shrub cover (Coates and Delehanty 2010), where predation effects were stronger when shrub cover was low. The prevalence of ravens on the landscape is also partially related to anthropogenic infrastructure, which subsequently affects sensitive prey species both directly and indirectly (Restani et al. 2001, Boarman et al. 2006, Marzluff and Neatherlin 2006, Kristan and Boarman 2007, Coates et al. 2014, O'Neil et al. 2018). Such factors and their context dependence are important to consider when weighing the costs of potential management options aimed at assisting populations of sensitive species such as sage-grouse or desert tortoise.

Importantly, we studied changes in total raven density in association with lethal raven removal efforts. The association between raven density and metrics of prey species reproductive success is complex, and prey responses may not always be correlated with raven density due to variation in the foraging behavior and breeding status of ravens. For example, Bui et al. (2010) found a stronger association between raven occupancy and sage-grouse nest success than with raven density. Resident ravens forage locally (Harju et al. 2018) and likely have better knowledge of surrounding food sources, and thus may be more likely to repeatedly depredate sage-grouse nests. While density is inherently correlated with occupancy, it is unlikely that all ravens within a population are frequent

predators of sage-grouse nests. Thus, reducing total raven density without specifically targeting those individuals most likely to depredate nests may not produce the desired improvement in sage-grouse nest success. This question remains relevant and important to sage-grouse conservation and raven management in sagebrush environments. Unfortunately, point count survey data are not adequate for identifying breeding status and foraging behavior because group sizes, reproductive status, and foraging behavior are either unobservable or not observed with high certainty. Understanding the predatory behaviors of ravens in relation to their breeding and/or reproductive status, as well as transient versus resident behaviors, likely requires monitoring marked individuals and studying their diets and foraging behaviors (Harju et al. 2018).

Although multiple factors influence the population dynamics of prey species such as sage-grouse, there is evidence that efforts to reduce predator densities can provide some amount of release. The relationship between raven density and sage-grouse nest success appears to be widespread in the Great Basin region (Coates and Delehanty 2010, Coates et al. 2020) and has also been documented in Wyoming where raven removal appeared to precede improvements in sage-grouse nest success (Dinkins et al. 2016). In addition, negative impacts to sage-grouse demographic rates from anthropogenic developments, such as high-voltage transmission lines, may in part be due to increased raven use and attraction to such features (Kristan and Boarman 2007, Howe et al. 2014, Gibson et al. 2018).

Raven impacts to sage-grouse nest success may be severe enough to alter local population dynamics, as sage-grouse growth rates from lek counts were associated with raven abundance near a high-voltage transmission line in Nevada (Gibson et al. 2018) and appeared to increase following raven removal efforts in Wyoming (Peebles et al. 2017). Management of raven populations may benefit multiple other species, though this relationship has not been thoroughly investigated aside from numerous studies inferring impacts to desert tortoises (Boarman 2003, Kristan and Boarman 2003, Shields et al. 2019, Berry et al. 2020).

Raven population densities exceed levels expected to influence sage-grouse population

dynamics over a significant portion of their range within the Great Basin region (Coates et al. 2020) and have not been directly quantified elsewhere. Impacts to species beyond sage-grouse and desert tortoises are possible but have received less research attention. Raven populations in this study appeared to exhibit continued increases at study sites that did not receive treatment. To address the ongoing issue of raven population increase and impacts to sensitive prey species, a suite of effective management strategies will likely need to be considered, and prescriptions of actions might largely depend on density of ravens and magnitude of their impact (Dettenmaier et al. 2021).

Our results indicated that the application of DRC-1339 at a local scale temporarily reduced raven numbers to levels below identified thresholds that minimize impacts to sage-grouse. The use of this action may be best suited for circumstances where elevated raven numbers have been deemed an immediate and substantial threat to sensitive prey. Effectively reducing the adverse effects of raven populations likely will depend on a variety of targeted management actions such as improving habitat quality for prey species, possibly reducing ravens' population density, and treating the underlying causes of increased raven abundance to reduce future carrying capacity and prevent population rebounds (Dettenmaier et al. 2021).

Management implications

We provide new evidence that sustained removal efforts from DRC-1339 can significantly reduce local raven populations, which implies temporary nest predation release for local sage-grouse populations and possibly other prey species, particularly when removal strategically targets specific sub-populations. We acknowledge the limitations of lethal removal when used as the sole management option where raven access to anthropogenic subsidies is not addressed. In the absence of other management actions to prevent population rebound from the source, if lethal removal is applied, then sustained effort would be required to maintain densities at levels deemed acceptable to mitigate predation effects on prey species, such as a 0.40 ravens km² threshold specific to greater sage-grouse population dynamics. Cost analyses may be useful to identify tradeoffs between

short-term efficacy of lethal removal relative to the costs of less direct management actions that may provide longer-term solutions by treating sources and subsidization of resources that promote raven population increase. Further, social acceptance will likely be an important factor for managers considering large-scale application of lethal removal. Our research demonstrates localized relative effectiveness of raven removal and informs its limitations. This improved understanding benefits landscape management planning for sagebrush ecosystems undergoing rapid anthropogenic change.

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Supplemental materials

Supplemental material can be viewed at <https://digitalcommons.usu.edu/hwi/vol15/iss3/20>.

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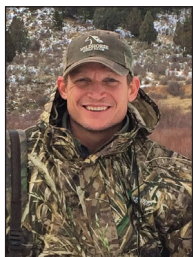
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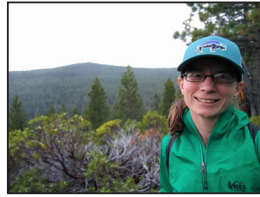
wolves in the Upper Peninsula of Michigan, USA. His work focuses on wildlife spatial and quantitative ecology with emphasis on greater sage-grouse habitat, population trends, and interactions with other overlapping species such as common ravens.

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