

## Case Study

# Efficacy of manipulating reproduction of common ravens to conserve sensitive prey species: three case studies

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**Abstract:** Expansion of human enterprise across western North America has resulted in an increase in availability of anthropogenic resource subsidies for generalist species. This has led to increases in generalists' population numbers across landscapes that were previously less suitable for their current demographic rates. Of particular concern are growing populations of common ravens (*Corvus corax*; ravens), because predation by ravens is linked to population declines of sensitive species. Ecosystem managers seek management options for mitigating the adverse effects of raven predation where unsustainable predator–prey conflicts exist. We present 3 case studies examining how manipulating reproductive success of ravens influences demographic rates of 2 sensitive prey species. Two case studies examine impacts of removing raven nests or oiling raven eggs on nest survival of greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) within Wyoming and the Great Basin of California and Nevada, USA, respectively. The third case study uses Mojave desert tortoise (*Gopherus agassizii*; tortoise) decoys to examine effects of oiling raven eggs on depredation rates of juvenile tortoises in the Mojave Desert in California. Initial trial years from all 3 case studies were consistent in finding improved vital rates associated with the application of strategies for reducing reproductive success of ravens. Specifically, removal of raven nests resulted in increased nest survival of sage-grouse within treatment areas where predation by ravens was the primary cause of nest failure. In addition, nest survival of sage-grouse and survival of juvenile tortoise decoys was higher following a treatment of oiling the eggs of ravens in their nests at 2 sites within the Great Basin and 4 tortoise conservation areas in the Mojave Desert in California. Along with specialized technologies that can make techniques such as egg-oiling more feasible, these findings support these management practices as important tools for managing ravens, especially in areas where breeding ravens have negative impacts on sensitive prey species.

**Key words:** *Centrocercus urophasianus*, common raven, *Corvus corax*, egg-oiling, *Gopherus agassizii*, greater sage-grouse, Mojave desert tortoise, nest removal, raven management, recruitment

**COMMON RAVENS** (*Corvus corax*; ravens) are opportunistic, omnivorous predators that occur across much of North America (Boarman and Heinrich 2020). Ravens can adjust to environmental changes readily, allowing them to exploit novel, anthropogenic subsidies within

otherwise natural environments. Expansion of human footprint in exurban and rural environments has resulted in greater access to anthropogenic resource subsidies for ravens across western North American landscapes (e.g., agriculture, electricity transmission infrastructure, and energy development), which were previously less suitable for their current rates of survival and recruitment (Boarman and Heinrich 2020). In areas where resources were otherwise limited, these subsidies are currently used by ravens for food, water, and nesting substrates (White and Tanner-White 1988, Knight et al. 1998, Webb et al. 2004, Boarman et al. 2006, Howe et al. 2014).

Increases in raven density and expansion of their distribution into areas that previously could not support large populations (Sauer et al. 2017, Harju et al. 2021) has implications for their prey species, which can be particularly problematic if their prey are of conservation concern. For example, large groups of young ravens subsidized by anthropogenic food and water sources may move into surrounding undeveloped areas and encounter sensitive prey, resulting in “spillover predation” (Kristan and Boarman 2003). Furthermore, because anthropogenic subsidies support increased abundances of territorial breeding ravens, their carrying capacity is decoupled from levels otherwise sustainable in the absence of subsidies in remote environments. This can lead to increased predation pressure, or “hyperpredation” (Smith and Quin 1996, Oro et al. 2013), on native and sensitive prey species within remote environments. Expansion and population growth of ravens has been increasingly linked to depressed population vital rates and declines in abundance of several sensitive species, such as greater sage-grouse (*Centrocercus urophasianus*; sage-grouse; Coates et al. 2020) and Mojave desert tortoise (*Gopherus agassizii*; tortoise; Kristan and Boarman 2003), among others (Coates et al. 2021a, Holcomb et al. 2021). Consequently, ecosystem managers responsible for the conservation and recovery of sensitive prey species are seeking management tools to suppress predation rates by ravens on already compromised prey populations to reverse, stall, or slow the progress of these species toward generational instability and local extirpation (Knight and Call 1980, Dettenmaier et al. 2021).

Efforts to reduce raven damage to local prey have included the lethal removal of adults and various behavioral aversion tactics (Avery et al. 1995, Coates et al. 2007, Peterson and Colwell 2014). However, several recent and ongoing management strategies intended to both limit raven recruitment in an area and decrease raven predation of sensitive prey focus on manipulating ravens during the breeding season, when they are confined to a nesting area. Breeding ravens establish territories (Webb et al. 2012), which allows them to efficiently target prey items in proximity to their nest sites. Territories typically average 3.2 km (Rösner and Selva 2005, Marzluff and Neatherlin 2006, Harju et al. 2018) from their nest sites, and ravens are known to forage intensively within these territories before and after hatching (Harju et al. 2018). During this reproductive period, predation rates on prey species are logically expected to increase due to the caloric demand of provisioning nestlings (average clutch size 3–7 eggs; Kelly et al. 2005, Brussee and Coates 2018). Management practices that reduce energetic needs of ravens during the breeding season and thereby reduce predation of eggs and young of sensitive species may improve vital rates of prey species in proximity to nesting territories of ravens.

Strategies for managing reproductive success of ravens include removing nests before or during the breeding season and oiling raven eggs to prevent hatch. These strategies have previously been shown effective at slowing population growth of problematic waterfowl (Wright and Phillips 1991, Beaumont et al. 2018), herring (*Larus argentatus*; Blackwell et al. 2000) and ring-billed gulls (*Larus delawarensis*; Engeman et al. 2012), double-crested cormorants (*Phalacrocorax auratus*; Dorr et al. 2003), and house sparrows (*Passer domesticus*; Fernandez-Duque et al. 2019). Nest removal involves removing a nest and all nest contents (i.e., nest structure, eggs and/or chicks) either prior to or during the breeding season. Egg-oiling is an addling technique, whereby food grade oil (e.g., mineral, vegetable, and silicone oils) blocks the eggshell’s gas-exchange pores and causes embryonic death by asphyxiation (Blokpoel and Hamilton 1989). Across previous studies, both nest removal and oiling treatments were generally successful (i.e.,

90–100%) at preventing successful hatch (i.e., reduced recruitment). However, few studies have assessed how these nest treatments impact nearby prey species (Johnson and Farquhar 2007, Brussee and Coates 2018).

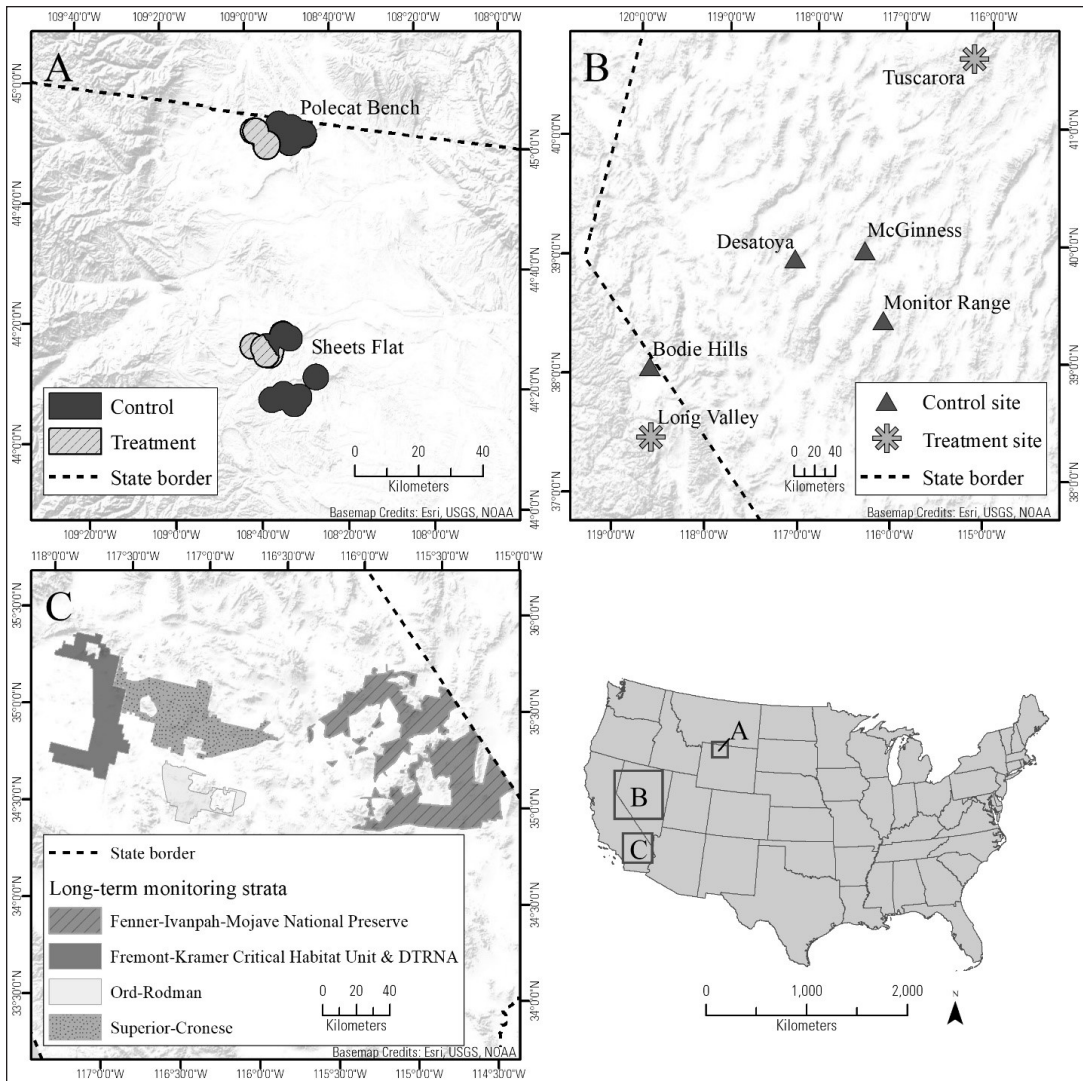
Here, we present initial results of 3 separate case studies with similar objectives of estimating the effects of removing raven nests or oiling raven eggs on productivity of 2 different prey species, sage-grouse and tortoise. Sage-grouse are a galliform bird of conservation concern because their abundance is decreasing throughout much of their range (Garton et al. 2011, Coates et al. 2021b). Coates et al. (2008) concluded that elevated raven numbers pose a substantial and widespread threat to nesting sage-grouse and likely impact population growth rates through nest predation (Peebles et al. 2017). Populations of tortoises inhabiting the Mojave Desert of California, USA, have declined precipitously since the 1980s (U.S. Fish and Wildlife Service [USFWS] 1994, 2010; Allison and McLuckie 2018). Threats to extant tortoise populations include anthropogenic disturbance, mortality from on- and off-road vehicles (Berry et al. 2008, Peaden et al. 2015), and increases in subsidized predators (USFWS 2011), such as ravens. Ravens are known to prey on juvenile tortoises up to an age of 10 years (108–134 mm mid-line carapace length; Turner et al. 1987), reducing recruitment rates of tortoises into reproductively mature age classes (Woodman et al. 2013, Hazard et al. 2015, Nagy et al. 2015). We chose to focus on these species because both are of conservation concern within 2 different ecoregions, and studies have revealed substantial impacts to both species by increasing abundances of ravens in the past 2 decades (Berry et al. 2013, Harju et al. 2021). Although the results from our case studies described here represent initial findings, collectively they may help to better inform strategies for managing ravens to protect sensitive species. These findings, as well as others published in this special issue on raven management, provide scientific underpinnings for management practices aimed at reducing predation on endangered species. Suggestions for incorporating either strategy into adaptive raven management frameworks, as well as specific informational needs from ongoing or future research, will be discussed.

## Study areas

### Case study I

The first case study estimated efficacy of common raven nest removal on nest survival of greater sage-grouse. The study was completed during 2016 and 2017 at 2 sites in northwest Wyoming, USA (Figure 1A), where a collaborative effort between Meeteetse Conservation District (Meeteetse, Wyoming, USA) and HWA Wildlife Consulting, LLC (Laramie, Wyoming) sought to investigate the efficacy of removing raven nests on nest survival rates of sage-grouse. Specifically, the Polecat Bench (PB) study site was located just north of Powell, Wyoming, and the Sheets Flat (SF) study site was located just east of Meeteetse, Wyoming. Previous work in this area by Taylor et al. (2017) determined that at the PB site, ravens were a primary sage-grouse nest predator, whereas at the SF site, ravens were a minor predator of sage-grouse nests.

Data were collected from a combined area of 600 km<sup>2</sup> with an elevation range of 1,280–1,890 m. Topography was moderately flat with intermittent buttes and small rolling hills surrounding the study area. The study areas have a semi-arid climate and experience all 4 seasons with average temperatures ranging from a low of approximately -4°C to a high of approximately 31°C near PB (Powell, Wyoming) and approximately -8°C to 27°C near SF (Meeteetse, Wyoming) between March and July. Vegetative communities consisted of shrubs dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and included rabbitbrush (*Chrysothamnus* spp. and *Ericameria* spp.), greasewood (*Sarcobatus vermiculatus*), birdfoot sagebrush (*A. pedatifida*), and big basin sagebrush (*A. t. tridentata*). Dominant grasses include western wheatgrass (*Pascopyrum smithii*), Indian ricegrass (*Achnatherum hymenoides*), needle and thread (*Hesperostipa comata*), bluebunch wheatgrass (*Pseudoroegneria spicata*), blue grama (*Bouteloua gracilis*), and Sandberg bluegrass (*Poa secunda*). Forbs include spiny phoxi (*Phlox hoodii*), desert parsley (*Lomatium* spp.), scarlet globemallow (*Sphaeroclea coccinea*), and Hooker's sandwort (*Arenaria hookeri*). Land use within this area was primarily focused on grazing by cattle (*Bos taurus*) and sheep (*Ovis aries*) with some areas involving oil and natural gas exploration and extraction.



**Figure 1.** Treatment and control sites located in (A) northwest Wyoming, USA, where common raven (*Corvus corax*; raven) nest removal occurred for studies of impacts to nest survival of greater sage-grouse (*Centrocercus urophasianus*) during 2016 and 2017; (B) the Great Basin of California and Nevada, USA, where raven egg-oiling occurred for studies of impacts to nest survival of greater sage-grouse during 2016–2019; and (C) the Mojave Desert ecoregion of California where raven egg-oiling took place for studies of impacts to predation rates of desert tortoise (*Gopherus agassizii*) decoys in 2020.

### Case study 2

Our second case study estimated the efficacy of oiling common raven eggs on nest survival of greater sage-grouse. This study represented a collaboration between U.S. Geological Survey (USGS) and Idaho State University (Pocatello, Idaho, USA) biologists to investigate the efficacy of oiling raven eggs as a management strategy to improve sage-grouse nest survival using a before-after-control-impact (BACI) study design across 6 study sites in the Great Basin to the Eastern Sierra mountains (Figure 1B) and

across years 2016–2019.

Study areas were located across multiple counties in California and Nevada, USA, and encompassed a combined area of 12,250 km<sup>2</sup> with an elevational range of 1,231–3,794 m. The study areas occurred in the Great Basin and Sierra Nevada mountains where the topography within the study areas typically included a mix of rugged mountains with rocky outcrops and broad valleys with a varying network of creeks. The vegetative communities were similar at all 6 sites and were primarily



composed of big (*A. tridentata* spp.) and low (*A. arbuscula*) sagebrush with some wooded areas mostly consisting of aspen trees (*Populus* spp.) and mixed species of pine trees (*Pinus* spp.). The presence and amounts of anthropogenic subsidies varied across each study area and typically included paved roads, utility lines, and cattle herding infrastructure. Average temperatures in these areas change by elevation and latitude, but they experience all 4 seasons with broadly warm summers and cold winters. Generally, they experience light rainfall (<50 cm) and heavy snowfall (>80 cm). Study areas were largely comprised of public land governed by the Bureau of Land Management (BLM) and U.S. Forest Service as well as some private land.

### Case study 3

The final study represented a collaboration between USFWS and USGS researchers to conduct an additional independent study of the effects of oiling raven eggs on “survival” of tortoises using 75 mm midline carapace length (MCL) tortoise decoys. Data for this study were collected between March 15 and July 1, 2020 within 4 separate critical habitat units designed for tortoises, located in the Mojave Desert of California (Kern, Los Angeles, and San Bernardino counties). Specifically, the study included the Fremont-Kramer Critical Habitat Unit and Desert Tortoise Research Natural Area, Fenner-Ivanpah-Mojave National Preserve, Ord-Rodman, and Superior-Cronese Areas (Figure 1C).

Study areas encompassed approximately 8,660 km<sup>2</sup> with an overall elevational range of 300–2,000 m above sea level. The terrain varied from flat valleys to sloping bajadas and interspersed mountain ranges. Dominant vegetation communities within the study areas consisted of creosote bush (*Larrea tridentata*) scrub and Joshua tree (*Yucca brevifolia* and *Y. jaegeriana*) woodlands. Weather patterns across the study areas form 4 regular seasons with temperatures near the geographic center of the study areas ranging from a low of approximately 6°C to a high of approximately 39°C between March and July. Annual precipitation in the same area averages 13.5 cm. Study areas were largely comprised of land managed by the BLM and U.S. National Park Service in addition to some private land.

## Methods

### Case study 1

*Sage-grouse nest monitoring.* During 2016, we captured sage-grouse almost exclusively on leks using rocket-nets, whereas during 2017, we used spot-lighting techniques (Wakkinen et al. 1992). We outfitted hens with 30-g solar-powered global positioning satellite (GPS)/ARGOS PTT transmitters (Microwave Telemetry, Inc., Columbia, Maryland, USA) using rump-mounted harnesses constructed with 0.635-cm Teflon ribbon (Bally Ribbon, Bally, Pennsylvania, USA). Sage-grouse capture and handling was approved by Wyoming Game and Fish Department Permit Number 33-1054. We programmed transmitters to record 16 GPS locations per day between April 15 and June 30, and the location data were transmitted via the ARGOS satellite system (CLS America, Inc., Lanham, Maryland) every 3 days. Sage-grouse nest locations were discovered by identifying clusters of GPS locations once nesting activity was detected (i.e., movement patterns indicative of incubation). We estimated the incubation date using GPS data, then forecasted the hatch date using an average incubation period of 27 days. A hen departing from a nest >2 days prior to the expected hatch date indicated a nest failure. We checked nests within 3 days after the hens departed the area to confirm nest fate. We considered nests successful if hens incubated for ≥24 days and a ground visit verified ≥1 egg hatched. Hatched eggs were identified by hatching pattern (i.e., eggs split transversely) and detached membranes.

*Raven nest removal.* Within the treatment portions of each study site, we established 4-km boundaries around GPS-tagged sage-grouse nests within which to conduct removal of raven nests (i.e., treatment). We altered the official delineation of each study site boundary where necessary to ensure that the treatment and control sides of each study site encompassed the associated GPS-tagged sage-grouse (Figure 1A). Within treatment areas, we conducted extensive searches for raven nests and once located, nests and associated eggs or chicks were removed or euthanized, respectively, as approved by the Wyoming Game and Fish Department (permit ID: 1056) and USFWS (permit # MB85114B-0). Treatment of raven nests took place throughout the overlap between the sage-grouse and

raven nesting seasons. All known raven nests in treatment portions were removed, and follow up surveys were conducted to monitor for re-nesting activity. On the control portions of each study site, we located but did not remove raven nests.

*Data analysis.* We modeled nest survival of sage-grouse using a Bayesian binomial model with a logit link function, with nest survival or failure specified as the response to predictors describing study site  $s$ , raven treatment  $t$ , and a study site by raven treatment interaction, as follows:

$$\text{logit}(\text{Nest.Surv}_i) \sim \beta_{st} \quad (1)$$

$$\beta_{st} \sim \text{Uniform}(-10, 10) \quad (2)$$

where  $\beta_{st}$  represents the interaction of site ( $s$ ; PB or SF) and nest removal treatment ( $t$ ; treatment or control). The site-by-treatment interaction produced 4 unique categories for the  $\beta$  parameter, which represented nest survival at each site-treatment combination. This model structure was appropriate because it allowed evaluation of differences in the effects of treatments at the 2 sites. We then used the posterior distributions of nest survival within each combination to calculate  $R$ -ratios (e.g., treatment to control) for each site. The ratio took the form:

$$R = \frac{S_T}{S_C} \quad (3)$$

where  $S_T$ ,  $S_C$ , represented sage-grouse nest survival within treatment areas and control areas, respectively.  $R$ -ratio values  $>1$  represented positive effects of treatment on nest survival.

Analyses were conducted in Program R version 4.0 (R Development Core Team 2018). The model was run on 15,000 iterations after an initial burn-in of 5,000. We retained 9,000 posterior samples for each parameter using 3 independent chains and thinning sampled iterations by a factor of 5. We evaluated chain convergence via visual inspection and requiring an R-hat Gelman statistic  $< 1.2$  (Gelman et al. 2014). We report mean values and 95% credible limits (CRL).

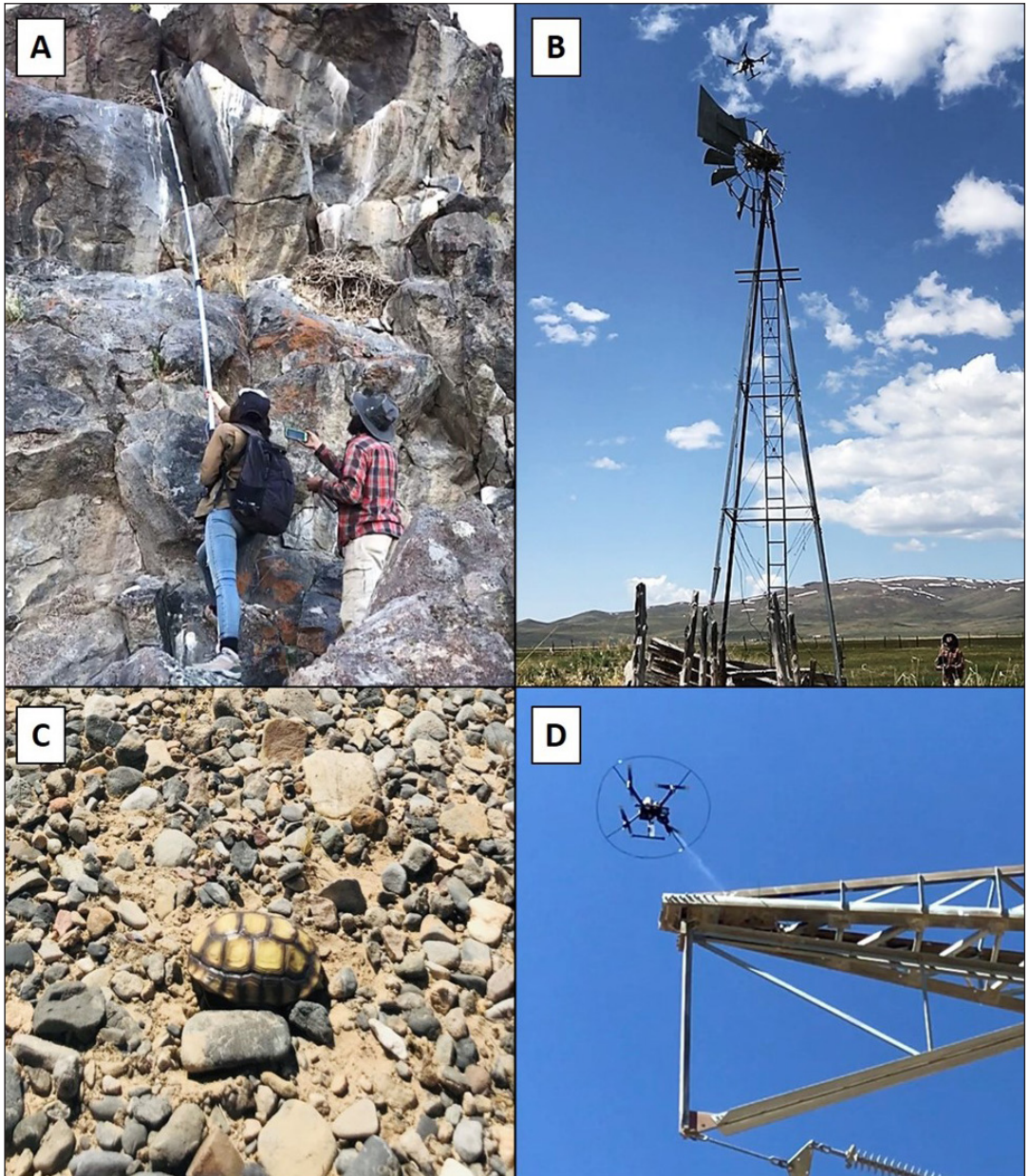
## Case study 2

During 2016–2018 (“before-treatment” period), we estimated nest survival of sage-grouse at all study sites and no site received egg-oiling

treatments. During 2019 (“after-treatment” period), raven eggs were oiled at 2 sites (i.e., treatment sites) and not oiled at 4 (i.e., control sites). Treatment sites were chosen based on a history of high raven presence and low nest survival for sage-grouse (USGS, unpublished data). Control sites were chosen based on their distance from the treatment site (i.e., the closest site possible) or similar anthropogenic features (i.e., geothermal plants) to the treatment sites. The BACI experimental design evaluates the change in nest survival under the egg-oiling treatment relative to the controls and, thus, offers evaluation of this action while accounting for natural temporal variability (Conner et al. 2016).

*Sage-grouse nest monitoring.* Nest survival data for sage-grouse were collected using the same methods across all study sites before and after raven egg-oiling treatments began. Briefly, we captured sage-grouse during the spring (March to April) and fall (August to November) and marked them with necklace-style very-high frequency (VHF; Advanced Telemetry Systems, Isanti, Minnesota, USA, and Holohil Systems, Ltd., Ontario, Canada) or rump-mounted GPS (GeoTrak Inc., Apex, North Carolina, USA) transmitters. During the spring, nesting hens were located using hand-held radio-telemetry equipment or GPS data. When nests were located using GPS data, a visit to that location was conducted to confirm nesting activity. Nests were checked every 3 days until a fate (i.e., hatched, predated, abandoned) was determined. Nests were considered successful if  $\geq 1$  egg hatched. All sage-grouse procedures were reviewed and approved by the USGS Western Ecological Research Center Institutional Animal Care and Use Committee, under IACUC protocol number USGS-ACUC-WERC-2021-FS-PC-Grouse-01.

*Raven egg-oiling.* During 2019, we also sought to locate raven nests within our study sites through visual inspection of anthropogenic structures, trees, and cliffs within each site (360–2,819 km<sup>2</sup>). Those efforts began in early March and continued through June to fully encompass the sage-grouse nesting season. Upon locating a raven nest, we viewed the nest-bowl and documented the presence or absence of eggs and chicks via a camera (Crosstour® CT7000) attached to a telescoping pole, or via use of an unmanned aerial vehicle (UAV; Phantom 4



**Figure 2.** (A) The use of a Remote Fluid Application System (RFAS) enabled telescoping pole for ground-based egg-oiling of common raven (*Corvus corax*; raven) nests. (B) The use of an RFAS-enabled drone to oil raven eggs in hazardous nests or nests >9 m off the ground. (C) A Techno-tortoise™ decoy used to detect a difference in predation rates of juvenile desert tortoises (*Gopherus agassizii*) by ravens. (D) The use of an RFAS-enabled drone to oil raven eggs on a power structure.

drone; DJI, Shenzhen, China). We checked nest phenology once per week to record clutch size and nesting behavior until hatchlings were observed or the adults abandoned incubation. For nests that occurred on transmission towers or private property that we could not access, we did not track nest phenology. If a nest was not viewable using our techniques, the behavior of

nearby adult ravens was documented (e.g., defending the nest, sitting in the nest, no ravens present) and used as a proxy to deduce nest phenology.

At treated raven nests, permitted by the California Department of Fish and Wildlife (permit number S-190200002-19022-001) and USFWS (permit numbers 93650B for California sites and



MB37116A-0 for Nevada sites), a silicone oil was applied to the upward-facing surface of each egg (Clearco PSF-5cSTT™; Clearco Products Co. Inc., Willow Grove, Pennsylvania). Oil application was targeted and delivered using either a ground-based or UAV-based Remote Fluid Application System (RFAS; Hardshell Labs Inc., Haines, Alaska, USA). Specifically, the ground-based method utilizes a telescoping pole, and the UAV method employs a drone to allow the oil to reach the eggs. Silicone oil is commonly used to addle eggs, as its non-toxic formula avoids unintended harm to incubating adult birds (Clearco 2015, Safety Data Sheet). We used ground-based methods when raven nests were located <9 m from the ground (Figure 2A). We used UAV-based methods to safely treat nests in hazardous locations or nests >9 m from the ground and utilized an RFAS-enabled UAV to spray raven eggs with oil (Figure 2B). We oiled raven eggs at both treatment sites during the first week of May when most nests were estimated to be in the egg-incubation stage and continued to check nests once per week following treatments until the adults abandoned the nests.

*Data analysis.* We used Bayesian shared frailty models (Halstead et al. 2012) in program JAGS 4.3 (Plummer 2017) utilizing R version 3.6.3 (R Development Core Team 2018) to estimate nest survival of sage-grouse assuming a 38-day egg-laying and incubation period. The unit hazard (UH) of each nest ( $n$ ) for each day ( $d$ ) was modeled as a continuous process observed at discrete, daily intervals and was expressed as:

$$UH_{[nd]} = \exp(\beta_{po} + \eta_i), \tag{4}$$

$$\beta_{po} \sim \text{Uniform}(-20, 0), \tag{5}$$

$$\eta_i \sim \text{Normal}(0, \sigma_\eta^2), \tag{6}$$

$$\sigma_\eta \sim \text{Uniform}(0, 10), \tag{7}$$

where  $\beta_{po}$  represented the interaction of period ( $p$ ; before or after treatment) and egg-oiling treatment ( $o$ ; oil applied or not applied), and  $\eta_i$  represented the random effect of hen ( $i$ ), respectively. The period-by-treatment interaction produced 4 unique categories for our baseline log hazard parameter ( $\beta$ ), which we refer to as BC (before-control), BT (before-treatment), AC (after-control), and AT (after-treatment).

The probability of survival ( $S$ ) for each nest was derived from the cumulative hazard ( $CH$ ) value using the equations:

$$CH_n = \sum_1^{D_n} UH_{1..d,n}, \tag{8}$$

$$S_n = e^{-CH_n}, \tag{9}$$

where  $D$  represented the total exposure period for each nest. The fate of each nest (*Nest.Surv*), coded 1 (successful) or 0 (failure), was modeled as a Bernoulli trial where the estimate of survival ( $S$ ) served as the probability of success:

$$Nest.Surv_{in} \sim \text{Bernoulli}(S_{in}) \tag{10}$$

Posterior probability distributions of nest survival were derived for each BACI group (e.g., treatment sites before, control sites before, treatment sites after, and control sites after) from our frailty model (i.e.,  $\beta_{po}$ ) and a 38-day egg laying and incubation period. To estimate the annual effect of egg-oiling at raven nests on the probability of nest survival of sage-grouse, we used the posterior distributions to calculate  $R$ -ratios of treatment to control sites before and after the onset of egg-oiling:

$$R_B = \frac{S_{BT}}{S_{BC}}, \tag{11}$$

and

$$R_A = \frac{S_{AT}}{S_{AC}}, \tag{12}$$

where  $S_{BT}$ ,  $S_{BC}$ ,  $S_{AT}$ , and  $S_{AC}$  represent nest survival estimates at treatment sites before (BT), treatment sites after (AT), control sites before (BC), and control sites after (AC) the onset of egg-oiling. A final BACI ratio distribution was calculated as the quotient of  $R$ -ratios from before and after periods:

$$BACI = \frac{R_A}{R_B} \tag{13}$$

We calculated additional control-impact (CI) measures (Chevalier et al. 2019) referred to as CI-contribution and CI-divergence, which took the form:

$$CI - \text{contribution} = |S_{AT} - S_{BT}| - |S_{AC} - S_{BC}|, \tag{14}$$

$$CI - \text{divergence} = |S_{AT} - S_{AC}| - |S_{BT} - S_{BC}|. \tag{15}$$



CI-contribution is used to estimate the degree of change by treatment site relative to control sites over the same time span, whereas CI-divergence seeks to quantify the degree of separation between control and treatment sites among periods. Both measures are important for gaining insight into the sources of change responsible for a BACI ratio above or below a value of 1 (i.e., no change).

The model was run on 50,000 iterations after an initial burn-in of 50,000. We retained 5,000 posterior samples for each parameter using 3 independent chains and thinning sampled iterations by a factor of 10. We evaluated chain convergence via visual inspection and requiring an R-hat Gelman statistic  $<1.2$  (Gelman et al. 2014).

### Case study 3

*Monitoring predation of tortoise decoys.* During the 2020 raven nesting season, we placed 19–20 tortoise decoy (3-dimensionally printed Techno-Tortoise™) stations, 0–2 novel object stations, and 0–1 camera-trap only station 250 m ( $\leq 10$  m) north of randomly placed point count locations throughout 4 separate management areas (78 total decoy stations, 4 novel object stations, and 4 camera-only stations; Figure 2C; Hardshell Labs, Inc., Joshua Tree, California) within each critical habitat unit to serve as a proxy for juvenile tortoises. All decoys measured approximately 75 mm MCL, roughly corresponding to the size of 5-year-old tortoises. All stations included a passive infrared motion-sensor triggered camera-trap (D300 Game Camera Kit, consisting of camera, SD card, and batteries; Moultrie Products, Birmingham, Alabama, USA) that was set up  $\sim 5$  m ( $\pm 2$  m) from the decoy. We deployed decoys between April 6 and April 17 and ended between April 22 and May 13, 2020 and sought to place them in open environments or at the edge of a shrub canopy (i.e., dripline). We then identified an appropriate area to install the camera-trap, which was programmed with a trigger delay of 00:00 and Mode of “3 Hi.” To expedite setup of decoy stations, we pre-mounted cameras on a 48-Inch Poly Step-in fence post cut to  $\sim 54$  cm (this places the camera lens at  $\sim 24$  cm above the ground) and painted with indoor-outdoor “satin oregano” spray paint and primer. When practicable, we deployed camera-traps near shrubs to maximize blending with the surrounding landscape

and to minimize exposure to direct sunlight. As the final step at each decoy station, we tethered the decoy or novel object to an anchoring stake, using a monofilament anchor tether. We attempted to conduct this last step as quickly as possible and then removed any footprints or other signs of our presence in the area before quickly leaving the area. This final step was performed as described to limit the time available for ravens, if present and watching, to associate the decoy with the person deploying it, as this type of association could potentially bias results. We considered decoys to be “depredated” if a raven was recorded within a 1.5-m radius of the decoy.

Concurrent with tortoise decoy survival trials, we also oiled all accessible and timely located raven eggs in each management stratum as approved by the California Department of Fish and Wildlife (permit number: S-19020002-19022-001) and the USFWS (permit number: 93650B). Similar to case study 2, we oiled eggs using an RFAS on telescoping poles and UAVs (drones; Figure 2D). Oil treatments were successfully applied to 0.08–0.71 of the estimated eggs available in each management area. A *post hoc* geospatial analysis was performed to measure the distance from each tortoise decoy to the nearest oiled nest. We performed a similar *post hoc* analysis of nearest potential unoiled eggs by using nest location records collected between 2013 and 2020 (USFWS, unpublished data). We used all previously located nests and not nests only located during 2020 because each year’s nest detection efforts are not designed to be exhaustive; therefore, using a collection of observations, including those from years when intensive searching was performed, ensured the inclusion of a maximum number of nests during a year of peak nest occupancy, such as 2020 in the Mojave Desert of California.

To estimate raven density, we followed survey methods described in Brussee et al. (2021). Briefly, we conducted 10-minute point count surveys at random locations within each study site during the raven nesting season. We also conducted a raven point count 250 m ( $\pm 10$  m) south of each camera station. At each survey, we recorded the survey location, number of ravens observed, distance to any observed ravens, and bearing using a GPS device, range-finder, and compass, respectively.

*Data analysis.* Raven density estimates for each critical habitat unit were derived from distance to raven cluster data recorded during point count surveys. Abundance and density estimation was conducted in Program R (R Development Core Team 2018) using package “distance,” version 0.9.7 (Miller et al. 2019), based on raven point count survey data. Data were binned every 250 m and truncated to 2 km because detection was considered low beyond this distance. We specified a hazard rate detection function, which accounted for decreasing detection at increasing distance up to 2 km (Buckland et al. 2001).

Similar to case study 2, we estimated the “survival” of tortoise decoys using a Bayesian shared frailty model (Halstead et al. 2012). The shared aspect refers to the frailties being common among individuals, in this case tortoise decoy stations, and the individual specific frailties being randomly distributed across the ensemble of decoy stations. Individual frailties were not of interest in this study but were fit to account for potential within-individual correlations that may have existed by way of study design and/or natural spatial heterogeneity. Specifically, some tortoise decoy stations experienced >1 predation event, which resulted in 2 or more trials for those stations (range = 1–5 trials per station; mean = 1.16; SD = 0.63). The application of random effects was advantageous here because it allowed us to bolster sample sizes by constructing an encounter history for each trial (i.e., the time between deployment and initial attack and between each subsequent attack) as opposed to each station, while explicitly accounting for the fact that predation events may not be independent within a single station.

Tortoise decoy “survival” was subsequently modeled as a function of egg-oiling treatment type to determine whether the practice of oiling raven eggs had a positive influence on tortoise survival. To account for confounding effects associated with density of ravens, we also included density as a covariate in the model. We utilized a daily encounter history and estimated the unit hazard ( $UH$ ) of each trial as:

$$UH_{td} = \exp(\alpha + \beta_{dist} * X_{dist} + \beta_{dens} * X_{dens} + \beta_{oil} * X_{oil} + \gamma_s), \quad (16)$$

$$\alpha \sim \text{Uniform}(-20, 0), \quad (17)$$

$$\beta_{dist} \sim \text{Normal}(0, 100), \quad (18)$$

$$\beta_{dens} \sim \text{Normal}(0, 100), \quad (19)$$

$$\beta_{oil} \sim \text{Normal}(0, 100), \quad (20)$$

$$\gamma_i \sim \text{Normal}(0, \sigma_\gamma^2), \quad (21)$$

$$\sigma_\gamma \sim \text{Uniform}(0, 10), \quad (22)$$

where subscripts  $s$ ,  $d$ , and  $t$  reference desert tortoise decoy station, day of study, and trial, respectively. Model parameters included a baseline log-hazard ( $\alpha$ ), random effect for tortoise decoy station ( $\gamma$ ), and log hazard ratios for raven density ( $\beta_{dens}$ ), egg-oiling ( $\beta_{oil}$ ), and distance to nearest raven nest belonging to the opposite treatment category ( $\beta_{dist}$ ). The distance parameter was meant to account for any potential confounding predation pressure not associated with the treatment group. In other words, we expected different survival rates for decoys within the egg-oiling treatment group depending on the natural log distance (m) to nearest non-oiled nest.

Similar to case study 2, we derived cumulative hazard ( $CH$ ) and probability of “survival” ( $S$ ) using equations:

$$CH_t = \sum_1^D UH_{1:d,t}, \quad (23)$$

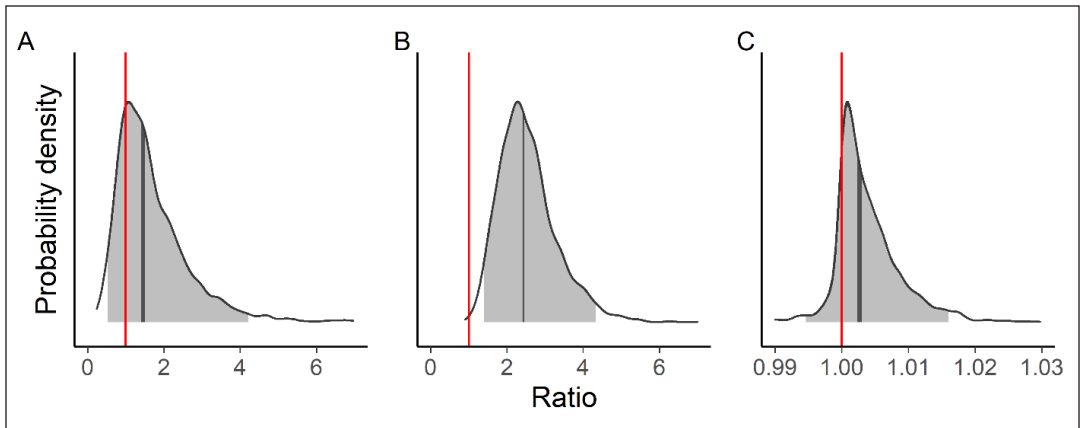
$$S_t = e^{-CH_t}, \quad (24)$$

where  $D$  represents duration of exposure period, in days, for each trial ( $t$ ).

The discrete outcome for each trial ( $y_i$ ) was coded 1 (undisturbed) or 0 (attacked) and served as the response variable for a single Bernoulli trial:

$$y_{it} \sim \text{Bernoulli}(S_{it}) \quad (25)$$

We estimated posterior distributions of cumulative probability of “survival” under a 1-day exposure period ( $S_{DETO}$ ) for each treatment category (i.e., oiled and non-oiled) given average raven density and distance to nearest raven nest. We created a treatment:control survival ratio by dividing posterior distribution from oiled nests to that of non-oiled nests to evidence the effect of oil treatment. A ratio >1 indicates that survival is greater in relation to



**Figure 3.** Results from 3 case studies that investigated the effect of oiling common raven (*Corvus corax*; raven) eggs on the survival of (A) greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) nests at 2 sites in Wyoming, USA, 2016–2017; (B) sage-grouse nests at 6 sites in the Great Basin of Nevada and California, 2016–2019; and (C) Mojave desert tortoise (*Gopherus agassizii*) decoys in the Mojave Desert, California, 2020. Ratios reflect the relative effect of raven nest removal treatments within (A) control and impact sites; raven egg-oiling treatments within (B) control and impact sites, before and after treatments were applied; and (C) control and impact decoy stations (assigned based on status of nearest raven nest). Strength of evidence is supported by the percent of the distribution  $>1$ , which was (A) 76.0%, (B) 99.9%, and (C) 89.1%. Gray shading represents the 95% credible limits of the ratio, and vertical black lines indicate the median of each ratio posterior distribution.

oiled nests compared to non-oiled nests.

Models were run using program JAGS 4.3 (Plummer 2017) and Program R (R Development Core Team 2018). The model was run on 10,000 iterations after discarding the initial 90,000 as burn-in. We retained 1,000 posterior samples for each parameter using 3 independent chains and thinning sampled iterations by a factor of 10. We evaluated chain convergence via visual inspection and requiring an R-hat Gelman statistic  $<1.2$  (Gelman et al. 2014).

## Results

### Case study 1

During 2016 and 2017, we monitored 42 sage-grouse nests. Specifically, we monitored 7 and 10 sage-grouse nests in the treated portions of the PB and SF study sites, respectively, and 16 and 9 sage-grouse nests in untreated portions of PB and SF, respectively. In the PB study area, 3 out of 11 nests and 4 of 12 nests were successful in 2016 and 2017, respectively. In the SF study area, 2 of 12 and 1 of 7 nests were successful in 2016 and 2017, respectively. In 2016, we located and removed 14 raven nests in treatment areas, and 11 nests were monitored in control areas but not removed. In 2017, we located and removed 5 raven nests in treatment areas. Eleven nests were monitored in control areas but not removed.

Overall, we found nest survival was higher at treated versus control areas of the study sites. Specifically, nest survival was 1.7 (95% CRL = 0.51–4.3) times higher at treated versus control areas, but 24% of the distribution was  $<1$  (Figure 3A). Within the PB study site, where ravens were determined to be the primary nest predator, we found sage-grouse nest survival was higher in the treated portion of PB (0.57; 95% CRL = 0.18–0.88) than in the control portion of PB (0.20; 95% CRL = 0.05–0.43). Specifically, nest survival was 3.91 (95% CRL = 0.87–12.7) times higher in treated versus untreated portions of the study area. Although 95% CRL for the ratio of nest survival at treatment versus control areas at the PB site overlapped 1, we found 95.9% of the posterior distribution was  $>1$ , indicating the probability of a positive effect of treatment was 95.9%. The same pattern did not hold for SF, where ravens were not the primary nest predator. In SF, nest survival was lower in treated areas (0.10; 95% CRL = 0.01–0.34) than control (0.22; 95% CRL = 0.03–0.52). Thus, the overall positive effect of nest removal treatments on sage-grouse nest survival was driven by the effect at the PB study site.

### Case study 2

During 2019, we monitored 37 raven nests (control = 19, treatment = 18) across all 6 sites. We



successfully oiled 13 nests within the treatment sites but failed to oil the remaining 5 because we either lacked private landowner permission ( $n = 1$ ) or nest fate (failed or hatched) occurred before oiling could be initiated ( $n = 4$ ). All 13 nests that received egg-oiling treatments resulted in complete nest failure (i.e., 0 eggs hatched). We did not observe any re-nests within the nests that were oiled, but we did not track ravens and, therefore, were unable to determine whether they re-nested at a new location.

We monitored 530 sage-grouse nests across 6 study sites from 2016–2019. The overall median probability of nest survival across all sites and all years was 0.38 (95% CRL = 0.33–0.45). At control sites, we monitored 253 pre-treatment and 100 post-treatment sage-grouse nests, of which 138 and 54 successfully hatched, respectively. The median probability of nest survival of sage-grouse at control sites, prior to egg-oiling treatments (2016–2018), was 0.35 (95% CRL = 0.29–0.43), which was similar to the post-treatment estimate in 2019 of 0.36 (95% CRL = 0.26–0.48). At treatment sites, we monitored 126 pre-treatment and 51 post-treatment sage-grouse nests. Of those, 50 successfully hatched during the pre-treatment period, and 35 successfully hatched during the post-treatment period. Median survival probabilities of sage-grouse nests were 0.23 (95% CRL = 0.16–0.32) prior to egg-oiling and 0.58 (95% CRL = 0.42–0.73) after egg-oiling treatments, which represents a 150% (95% CRL = 60–287%) increase in survival probabilities from before to after treatments.

A final BACI ratio of 2.44 (95% CRL = 1.39–4.33) was calculated based on  $R$ -ratios from before (median  $R_B = 0.65$ , 95% CRL = 0.43–0.95) and after (median  $R_A = 1.59$ , 95% CRL = 1.05–2.39) periods, which represents an increase in probability of nest survival of sage-grouse of 144% (95% CRL = 39–333%) in the treatment group relative to the control (Figure 3B). We found 99.9% of the distribution of the effect was  $>1$ , indicating a 99.9% probability of a positive effect of egg-oiling on sage-grouse nest survival. Our CI-contribution estimate provided additional information about the source of improvement in nest survival rates. Namely, increases in nest survival were substantially larger at treatment sites compared to control sites over the same period of inference (median CI-contribution = 0.29, 95% CRL = 0.09–0.46). The CI-divergence

estimate, which is used to evaluate the degree of dissimilarity among treatment and control sites across the 2 periods of inference, provided marginal evidence of greater separation between treatment and control sites during the after period compared to the before period (median CI-divergence = 0.09), but with a 95% CRL that overlapped 0 (-0.11 to 0.30).

### Case study 3

We used data from 78 stations in this analysis (oiled = 12, non-oiled = 66). Each time when a decoy was “attacked,” a new trial began. We used 100 trials in the analysis (oiled = 14, non-oiled = 86).

We estimated median tortoise daily survival to be 0.999 (95% CRL = 0.987–1.000) in proximity to oiled nests and 0.996 (95% CRL = 0.981–1.000) in proximity to non-oiled, frequently occupied nest territories. The ratio of oiled to non-oiled “survival” was estimated to be 1.003 (95% CRL = 0.995–1.016), representing a median increase in daily “survival” probability of 0.33% in proximity to oiled raven nests (Figure 3C). We found 89.1% of the posterior distribution for the ratio parameter was on the same side as the median, indicating the probability of an effect of egg-oiling on tortoise survival was 89.1%. Importantly, this median daily increase in survival amounts to a substantial increase in cumulative survival probability on an annual basis. For example, under a 129-day exposure period (e.g., approximate average length of time for incubation, pre- and post-fledging and final natal dispersal; Webb et al. 2009, Cornell Lab of Ornithology 2019), median “survival” probability increased by 53% at oiled nests compared to non-oiled nests. We also found that the log hazard ratio increased (i.e., lower survival) with increased raven density ( $\beta_{dens} = 0.79$ ; 95% CRL = -0.66 to 3.28). While the credible intervals overlapped 0 for this effect, 86% of the distribution was positive, indicating an 86% probability of lower tortoise survival with increased raven density. In addition, increasing distance to the nearest raven nest of the opposite treatment group resulted in decreased hazard (i.e., higher survival;  $\beta_{dist} = -0.00054$ , 95% CRL = -0.00136 to -0.00008). The credible limits of this effect did not overlap 0, which demonstrates the importance of creating separation between ravens and tortoises to avoid unsustainable predator–prey conflicts.

## Discussion

These 3 case-studies' initial findings were consistent regarding the efficacy of raven nest removal and egg-oiling treatments as novel management actions that reduce reproductive success of ravens and result in decreased predation to sensitive sage-grouse and tortoise species within 2 different desert ecosystems. Specifically, raven nest removal and egg-oiling resulted in increased nest survival of sage-grouse within treatment areas where raven depredation was the primary cause of nest failure for sage-grouse. In addition, juvenile tortoise decoy "survival" was higher following raven egg-oiling throughout 4 sites in the Mojave Desert in California. For the tortoise study, it is important to acknowledge that decoys served as a proxy to measure juvenile tortoise survival and that vital rate was not directly measured. The use of a desert tortoise 0- to 10-year-old proxy is necessitated by the challenges of consistently locating live tortoise in these age classes (Allison and McLuckie 2018). Even so, findings from these recent studies support that egg-oiling and nest removal may be important tools for managing predation by ravens as well as raven densities and could aid in the development of conservation as well as recovery strategies for species sensitive to raven depredation. Additionally, these studies corroborate previous findings supporting the use of egg-oiling and nest removal as a management tool capable of reducing impacts of predation by ravens (USFWS, unpublished data; Brussee and Coates 2018).

Utilizing nest removal and egg-oiling to curtail successful reproduction by ravens may directly reduce predation rates by ravens by removing the caloric demand of provisioning nestlings (Kelly et al. 2005). These management strategies are also expected to elicit treatment-specific behavioral changes from breeding pairs of ravens, which may incur additional effects on nearby prey. For example, nest removal may induce changes in movement patterns of birds whose nests were removed, causing them to leave a study area sooner than birds that successfully produced chicks (Beaumont et al. 2018). Specifically, following a nest failure, raven pairs switch from intensive foraging around the nest to opportunistic foraging across the landscape, and they increasingly rely

on anthropogenic subsidies (Harju et al. 2018). As a result, removal of raven nests may improve survival of prey species by inducing a fundamental change in foraging behaviors of ravens and how they use the landscape. However, this change in territorial behavior of breeding ravens following nest removal could also result in influx of transient ravens into what was previously a breeding territory (Kristan and Boorman 2003). In contrast, breeding birds whose nests are treated with egg-oiling often continue incubating nests past the estimated hatch date (Atkinson et al. 2020), maintaining and defending their territory against transient ravens. Where maintenance of the territory is ideal, egg-oiling can provide an effective management option for reducing predation by ravens. The most effective treatment for managing reproductive success of ravens will likely vary depending on phenology of local raven populations, effects of other predator species on the demographic rates of prey intended to benefit from managing raven nests, and site characteristics including accessibility and presence of anthropogenic subsidies.

Egg-oiling and nest removal are management actions that target breeding ravens. Thus, understanding the composition of particular raven populations (i.e., resident vs. transient birds vs. breeding season meta-populations) and other predator species may inform the most appropriate management prescriptions. For example, egg-oiling may provide greater protection to sensitive prey populations inhabiting areas closer to subsidized point sources (i.e., landfills, commercial agriculture, water treatment facilities, decorative ponds, etc.) by maintaining defense of breeding territories by nesting pairs. Maintaining raven territories may reduce their non-breeding and breeding density (Avery et al. 1995, Webster et al. 2021) and ultimately reduce effects of spillover predation (Kristan and Boorman 2003, Bui et al. 2010). Conversely, in areas with lower concentrations of breeding and non-breeding ravens or in source habitat of sensitive species, nest removal may have greater success in management of raven impacts. Nest removal is also useful later in the reproductive season when egg-oiling is no longer an option. Furthermore, egg-oiling may be undesirable on structures such as transmission towers, where keeping raven nests intact may cause electri-

cal faults, fires, outages, and liability to utility companies (Restani and Lueck 2020). On these structures, nest removal may be preferable because it removes potentially hazardous nesting materials.

From a hazard-control perspective, removing raven nests immediately upon locating them may be the most effective strategy for reducing the chances of the nest material causing a fire or electrical issue. This may occur prior to the breeding season on nests that can be reused in the future or in the very early stages of the breeding season during nest construction or egg-laying. Yet, from a biological perspective, the most effective approach for reducing raven re-nesting activity is believed to be when nest removal treatments are applied closer in time to high parental investment by breeding ravens, such as in the late egg-incubation or chick stages. Removal techniques may lose effectiveness when they occur too early or outside of the nesting season (Gates et al. 2013, Claassen et al. 2014), as ravens readily rebuild nests immediately prior to nesting. Furthermore, if timed too early, nest removal could result in re-nesting behavior, necessitating continued monitoring and treatment efforts. For all management strategies, understanding the timing of raven nest initiation will influence the decisions to oil eggs, destroy nests, or continue monitoring.

It is important to note that both nest removal and egg-oiling necessitate intensive effort. In the case of limited resources, deciding which nests to prioritize might include factors such as accessibility, proximity to roads, etc. For example, an easily reached nest may be left for further monitoring and later oiling, but a remote nest may be oiled if continued monitoring is deemed too costly. In our tortoise case study, we found evidence that daily survival was improved in proximity to oiled nests relative to non-oiled nests. Therefore, targeting nests closest to prey species of interest would be most effective at reducing predation and would be a way to prioritize and efficiently distribute workload. Additional considerations are needed for nests on artificial structures or on private property, which may require special arrangements with property owners. Lastly, study site characteristics, such as topography, surface texture, and accessibility may make both treatment types difficult to apply in some areas. However, the

ability to access hard-to-reach nests for egg-oiling has been partially alleviated with the recent introduction of RFAS poles and drones (Shields et al. 2019), which were used in the egg-oiling case studies presented here.

The first and third studies were not designed within a BACI framework and, thus, initial findings should be interpreted with caution. However, the consistency in results across all 3 studies substantiates the overall finding that manipulation of raven reproduction via egg-oiling or nest removal increases reproductive output of sensitive species. Additionally, these 3 studies consisted of only 1 or 2 years of treatment and, therefore, cannot contribute information about long-term efficacy of these management strategies. For example, following a nest failure, ravens may not nest in the same location (Haas 1998), which has implications for successful management. During a 6-year study on Alcatraz Island (California), Brussee and Coates (2018) found that during years following egg-oiling, ravens did not nest on the island, and black-crowned night heron (*Nycticorax nycticorax*) nests experienced higher survival rates than when ravens were nesting. Furthermore, annual egg-oiling practices within the Mojave Desert resulted in near total abandonment of a 12.9-km<sup>2</sup> site (T. A. Shields, Hardshell Labs Inc., unpublished data). This evidence suggests that manipulating raven breeding success may result in ravens abandoning study areas, potentially moving into areas with reduced chances for predator–prey conflicts. However, more information is needed to verify that ravens are not simply consuming sensitive prey at newly established nesting areas.

Camera monitoring of tortoise decoys substantiated evidence that ravens are an important predator of live juvenile tortoises (Hazard et al. 2015, Nagy et al. 2015), and previous site-level studies utilizing camera monitoring found ravens to be the primary predator of sage-grouse (Coates and Delehanty 2010, Lockyer et al. 2013). However, it is unclear whether territorial or transient ravens are more responsible for reduced vital rates of prey. Although transient ravens individually may not be as efficient a predator as territorial ravens, at high densities, such as areas surrounding anthropogenic point sources or communal roosts, they could have strong impacts on prey species



(e.g., spillover predation; Kristan and Boarman 2003). In the desert tortoise case study, predation risk to tortoises across the California Mojave Desert increased with increasing raven densities and decreasing distance to previously active raven nest (Holcomb et al. 2021). Furthermore, in a large-scale study spanning the Great Basin, Coates et al. (2020) found decreased nest survival of sage-grouse related to high raven densities. High densities of ravens are likely associated with much greater proportions of transient ravens (i.e., non-breeders), which tend to congregate in larger groups, and for which the management strategies presented here would not apply. When transient ravens are primarily responsible for predator-prey conflicts within a study area, additional management strategies that reduce existing numbers of juvenile and adult ravens (O'Neil et al. 2021) might be immediately beneficial to protecting sensitive species (Dinkins et al. 2016, Peebles et al. 2017). Additionally, survival of sage-grouse nests and desert tortoises can be impacted by other predator species such as coyotes (*Canis latrans*) and badgers (*Taxidea taxus*; Coates et al. 2008, Emblidge et al. 2015, Kelly et al. 2021). We learned that these strategies for managing ravens may be less effective in areas where other non-targeted predators are the primary source of low prey demographic rates, as was observed at the Sheets Flat site in Case study 1.

If raven predation constitutes a small portion of depredation instances, we might expect a proportionally small effect on improved prey survival following raven nest treatments. Importantly, at sites where predation by ravens results in unsustainable predator-prey dynamics, continued application of nest removal or egg-oiling strategies at a site over multiple years will likely slow population growth of ravens and ultimately reduce raven abundance (see Currylow et al. 2021). Availability of more tools for raven management, such as egg-oiling and nest removal, enables development of more customized management plans for reaching conservation and recovery goals.

Previous studies have identified several different strategies for managing ravens, which have generally had some success at reducing raven presence and damage to local wildlife while being applicable for both breeding and transient ravens. For instance, lethal removal of

adult ravens resulted in the decreased presence of ravens as well as improved rates of nest survival rates of their prey within a managed area (Coates et al. 2007, Dinkins et al. 2016) but is limited in feasibility due to legal and sociopolitical challenges and issuance of permitting through the Migratory Bird Treaty Act (Boarman 1992). Using behavior modification strategies such as the use of effigies, lasers, or taste deterrents to create a behavioral aversion response in ravens have shown variable success in reducing raven presence and damage to colonial nesting birds (Avery et al. 1995, Blackwell et al. 2000, Peterson and Colwell 2014) and may be used to deter ravens from specific areas. These strategies could potentially be used in conjunction with raven egg-oiling and nest removal to further improve prey survival.

### Management implications

With continued expansion of human enterprise into remote environments, we anticipate that raven population expansion will continue to result in overlaps with sensitive prey species, emphasizing a need to assess novel strategies for managing ravens that work under various and dynamic scenarios. Our results indicate that successful management of raven densities and the impacts of ravens will likely require a balance of targeted, short-term management actions of breeding ravens as well as non-breeding transient ravens using long-term reduction of access to anthropogenic resource subsidies and prey habitat restoration efforts (Dettenmaier et al. 2021). Nevertheless, these 3 studies suggest that egg-oiling and nest removal may be effective tools for managers to consider when specific predator-prey conflicts exist between breeding ravens and vulnerable species.

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