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Common raven movement and space use: influence of anthropogenic subsidies within greater sage-grouse nesting habitat

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Abstract. Common raven (*Corvus corax*; hereafter "raven") populations have increased dramatically in the western United States in recent years. Ravens benefit from human resources and are known predators of other avian species. We developed a raven study to determine how primary (large-scale, high food density, and temporally consistent) anthropogenic subsidies influenced raven movement and space use during the raven and greater sage-grouse (*Centrocercus urophasianus*) breeding season and within sagebrush habitat that is commonly used by greater sage-grouse. We also examined how movement, space use, and anthropogenic subsidization differed among ravens in different breeding statuses. We hypothesized that breeding ravens would use small areas around their nest and that nonbreeding ravens would range widely in search of food. We expected that breeding ravens would frequently use anthropogenic structures and that both breeding and nonbreeding ravens would regularly visit primary point-source subsidies (e.g., landfills and transfer stations). Twenty ravens were captured and GPS-tagged between 2012 and 2014. We found that breeding ravens overwhelmingly built nests on anthropogenic structures (96–100%) and subsequently used small portions of the landscape intensively. Movement of nonbreeding ravens (distance average = 2783 m/h) and ravens who had failed nests (distance average = 1357 m/h) ranged widely. Breeding ravens visited highways and railroads inversely proportional to the distance between the nest and the nearest highway/railroad. Nonbreeding ravens regularly visited landfills and transfer stations, but breeding ravens did not (<0.1% of locations). We found that nonbreeding ravens travel widely to utilize primary point-source subsidies, breeding ravens focus on areas near the nest, and ravens with failed nests switch to movement behaviors and space use similar to wide-ranging nonbreeding ravens. These findings have implications for the management of ravens and anthropogenic subsidies in sagebrush landscapes to potentially reduce depredation of greater sage-grouse nests.

Key words: anthropogenic food subsidies; common raven; conservation planning; *Corvus corax;* generalized linear mixed models; greater sage-grouse; raven movement; shrub-steppe; space use; Wyoming, USA.

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Introduction

Common raven (*Corvus corax*; hereafter raven) populations have increased dramatically in the western United States over the past four decades (Sauer and Link 2011). This is largely due to the increase in scale by which ravens are inadvertently subsidized by anthropogenic resources. Ravens benefit from human resources such as increased access to discarded food (Kristan et al. 2004), food subsidies via road-killed animals, shelter in abandoned structures (e.g., buildings),

access to water impoundments in arid landscapes, nesting substrates in landscapes that previously did not contain suitable natural structures (Steenhof et al. 1993), and from historic anthropogenic reduction in raven predators and competitors (Wilmers et al. 2003).

The increase in raven populations creates a number of concerns for humans and wildlife alike. Concerns include health and safety issues with abundant raven feces around nests, and damage to domestic sheep and cattle operations, and ravens are known predators of other bird nests including birds of conservation concern (Stiehl and Trautwein 1991, Kelly et al. 2005, Marzluff and Neatherlin 2006, Coates et al. 2008). These concerns are widespread across a variety of habitats, in the western United States alone ranging from the Mojave Desert (Kristan and Boarman 2007) to temperate rainforest (Marzluff and Neatherlin 2006) to sagebrush-steppe (Peebles et al. 2017). Specific to sagebrush-steppe, there is general concern on the impact of subsidized avian predators on native species, but also specific concern about the effects of raven subsidization on greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) breeding populations. Sage-grouse have recently been petitioned and considered for potential listing under the U.S. Endangered Species Act (USFWS 2008, 2010). The U.S. Fish and Wildlife Service (USFWS) determined that sage-grouse were not warranted for listing in 2015; however, sage-grouse remains a species of conservation concern across their range in the western United States (USFWS 2015). Nesting success of sage-grouse has been noted as a key factor driving sage-grouse population dynamics (Connelly et al. 2000, Taylor et al. 2012). Previous research has also found that when sage-grouse nests fail, predation is the source of failure between 82.5% and 94.0% of the time (Moynahan et al. 2007, Lockyer et al. 2013). Ravens are known sage-grouse nest predators, accounting for as much as 46.7–58.8% of nest depredations (Coates et al. 2008, Lockyer et al. 2013). Ravens have also been documented removing and caching sage-grouse eggs for later consumption (Howe and Coates 2015). Thus, by being a fundamental driver of sage-grouse population dynamics (Taylor et al. 2012), factors supporting subsidized nest predators (e.g., ravens) are of interest to wildlife managers and ecologists.

We developed a new raven study in sage-grouse nesting habitat with the goal of quantifying how primary (large-scale, high food density, and temporally consistent) anthropogenic subsidies influenced raven movement and space use during the raven breeding season. A second goal was to determine how movement, space use, and anthropogenic subsidization differed among ravens in different breeding statuses. We hypothesized that breeding ravens would use small areas around their nest and that nonbreeding ravens would range widely in search of food. We expected that breeding ravens would frequently use anthropogenic structures as nesting substrates and that both breeding and nonbreeding ravens would regularly visit primary point-source subsidies (e.g., landfills and transfer stations). Because this study occurred within sage-grouse breeding habitat and was primarily motivated by a desire to better understand raven subsidization in sage-grouse breeding habitat, we discuss the findings with respect to sage-grouse ecology. However, the results from this study reflect general raven ecology and may be relevant to a wide range of ecosystems where managers deal with raven issues.

Methods

Study area

Our study area, located near Creston Junction in eastern Sweetwater County, Wyoming, encompassed approximately 2700 km^2 (Fig. 1). The habitat was predominantly sage-steppe habitat and consisted of flat to moderately rolling terrain. High-quality nesting habitat for sage-grouse comprised the majority of the study area, and sage-grouse were relatively abundant throughout the area. A total of 35 occupied sage-grouse leks occurred within the study area including several with 30–50 males (WGFD, *unpublished data*). Approximately 44% of the study area fell within a designated sage-grouse core area (Wyoming Core Area Policy, State of Wyoming, 2015). The study area was located in a region that has undergone extensive energy development over the past 15–20 yr, and development of oil, natural gas, and uranium resources is ongoing. Subsequently, the majority of the anthropogenic features across the landscape were related to the energy industry, including improved gravel

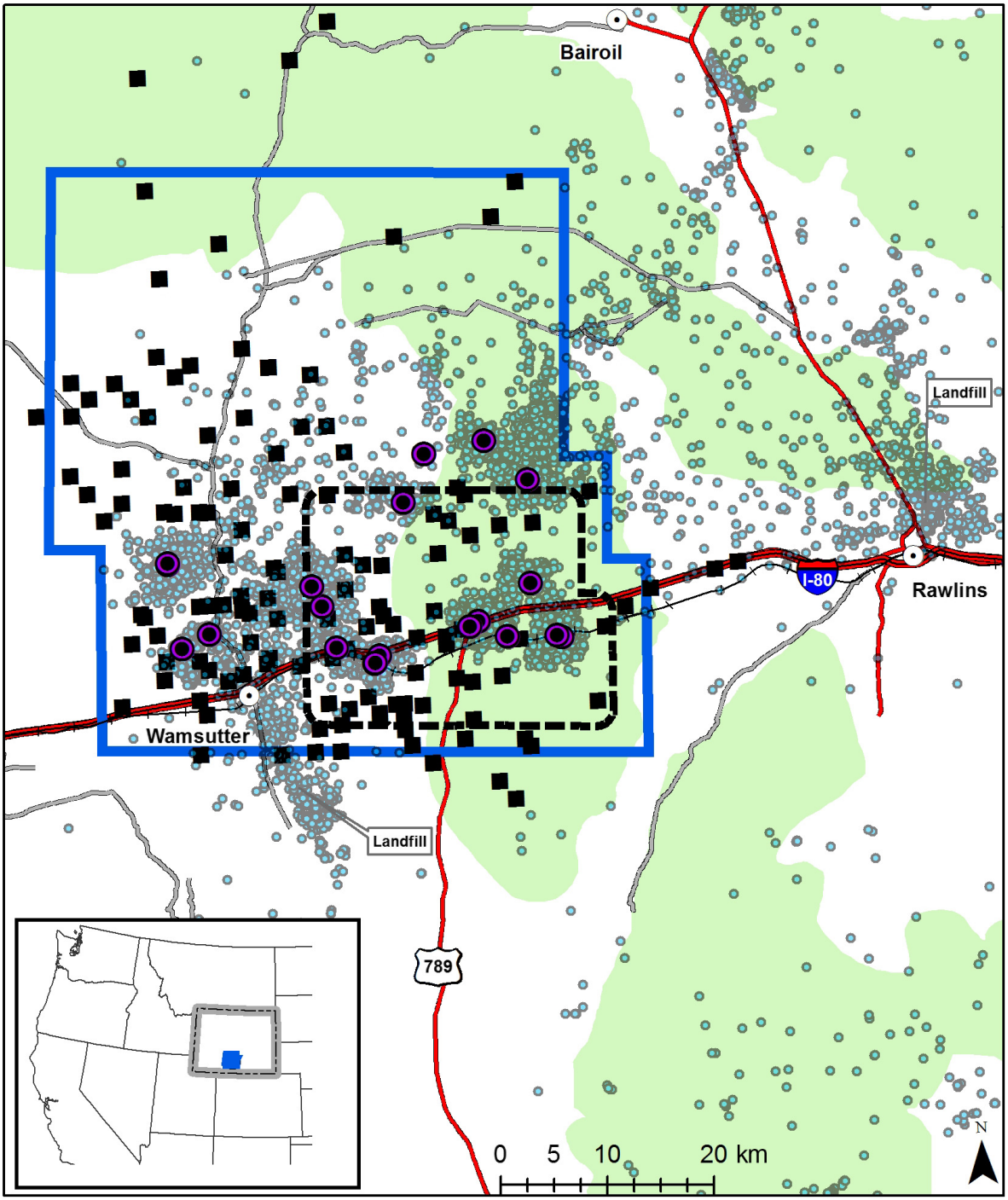

Fig. 1. Study area (blue) used to investigate common raven movement, space use, and use of anthropogenic subsidies in south-central Wyoming, USA, 2012–2014. Locations of ravens equipped with GPS transmitters are small green circles, GPS raven nests are purple circles, and raven nests by non-GPS birds are depicted by black squares. The dashed polygon is the nest census area, where comprehensive surveys of all nesting substrate for active and inactive raven nests were conducted 2012–2014. Wyoming greater-sage-grouse core area is depicted by the green-shaded area.

roads, well pads, overhead distribution power lines, pipeline rights-of-ways, and various ancillary facilities and structures (e.g., compressor stations). Evaporation ponds and water injection wells were largely used for disposing of produced water in the study area, although these sites were limited (small energy-related ponds were rare to nonexistent in the study area). Within the study area, infrastructure associated with energy development occurred along a gradient ranging from fairly extensive in the southern portion to nonexistent in the north. Other anthropogenic features included an interstate highway (I–80), Wyoming State highway (WY789), overhead transmission power lines, railroad corridor, and several communication towers. Features associated with ranching and sheep grazing were also present, including windmills, water tanks, barns and outbuildings, and corrals. Cattle were free-ranging and were present in the late-summer months. Ravens were common throughout the study area.

Capture and monitoring

Ravens were captured using a variety of methods (net launchers, noose carpets, hoop nets, mist nets, and dho-gaza nets), but the majority of birds were netted at roosting locations or captured using bait and remote-controlled net launchers (Trapping Innovations, Kelly, Wyoming, USA). Captured ravens were equipped with 30-g solar ARGOS/GPS PTT transmitters (PTT–100; Microwave Telemetry, Columbia, Maryland, USA) using backpack mounts with ¼″ Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania, USA). Transmitters were programmed to record 10–15 GPS-quality (±18 m) locations per day for each bird, depending on the time of year, and the location data were received via the ARGOS satellite system (CLS America, Lanham, Maryland, USA) every three days.

Nest substrate

Simple quantification of whether raven nests are built on anthropogenic structures vs. natural features provides a coarse measure of how human activities can enhance nest occurrence in areas with otherwise limited natural features to support raven nests, such as sagebrush-steppe. We located and documented active nest structures for GPS-tagged ravens. We also conducted comprehensive surveys of all nesting substrate for active and inactive raven nests within the nest census area, comprising a smaller but representative portion of the study area, and opportunistic surveys within and around the remaining portion of the study area from 2012 to 2014 (Fig. 1). Although we considered them opportunistic because we did not fully census the study area, our extensive amount of time in the field combined with conspicuous elevated raven nest placement suggests that we found the majority of active raven nests present (Dunk et al. 1997). We recorded the location of active nests using handheld GPS units. We recorded nest substrate (i.e., the object/material on which the nest was located) and classified the substrate as either human-made or a natural feature.

Note that we did not quantify the availability of natural nesting substrates because of the difficulty and subjectivity in determining which individual substrates could hypothetically be used by ravens in the absence of anthropogenic structures and the density of raven territories that would be supported.

Breeding status

Our primary focus was on breeding status of ravens, and how anthropogenic nest substrate and major, consistent food subsidies were related to raven space use and movement metrics for ravens in different breeding statuses. First, we designated the breeding season for all ravens within each year as six days before the earliest date that any raven began incubation until 14 d after successful fledging of the latest breeding raven (Stiehl 1985). We only considered GPS locations for ravens of any breeding status within this window within each year to avoid comparing seasonally varying movement behaviors of nonbreeding birds with movement behaviors of breeding birds (Loretto et al. 2015). Second, we considered four temporally mutually exclusive breeding statuses to which we assigned each raven GPS location: breeding, post-failed nest, post-successful nest, and nonbreeding. A raven was considered as breeding beginning six days pre-incubation until either 14 d post-fledging or 1 d post-nest failure. Incubation and fledging/failure dates for each breeding raven were determined via monitoring of GPS locations and field observations. Nest surveys were conducted

approximately every two weeks between late March and mid-June for documenting nests, including re-nesting attempts, and active nests were monitored until nests failed or chicks fledged. A successful nest was defined as a nest that fledged at least one chick. A "failed" nest was considered a nest that failed to produce an offspring to fledgling age. A single breeding raven could be part of up to two breeding statuses within each year: breeding + post-failed nest or breeding + post-successful nest. Due to raven GPS-fix gaps or timing of nesting within the general breeding season, some ravens were only part of the breeding status in a year. Non-breeding ravens did not breed at all within that year. Some ravens were monitored for multiple years. From here, we refer to each set of GPS locations within an individual raven and year as a bird-year.

Anthropogenic subsidies and space use

With relation to raven space use during the breeding season, we delineated two sources of potential anthropogenic food subsidies: highway/railroad and primary point-source subsidies. Highways/railroads provide anthropogenic sources of food via roadkill and, to a lesser extent, trash litter (Kristan et al. 2004). Point-source subsidies provide an abundant source of discarded food and trash for ravens and other scavengers (Kristan et al. 2004). The highway-railroad category included Interstate 80, State Highway 789, and an active railroad that runs east–west, roughly parallel to Interstate 80 (Fig. 1). Preliminary inspection of the raven GPS data showed the same pattern of use of the railroad as the highways; therefore, we considered both the railroad and highways as the same type of anthropogenic food subsidy. We did not include maintained gravel or two-track roads as potential sources of anthropogenic subsidy because their role as a direct subsidy was likely small given their smaller size, slower traffic speeds, and considerably lower traffic volumes. Examination of the GPS data indicated that our measurement metric (i.e., GPS locations) was not associated with these road types. We note that livestock (cattle or sheep) were not used as a subsidy variable due to the unpredictable spatial and temporal characteristics of the subsidies associated (carcasses and calving) with the operations in the study area.

To delineate point-source subsidies, we used our experience within the study area and aerial imagery to heads-up digitize landfills and transfer stations within the study area. For both highways/railroads and point-source subsidies, we added a 100 m buffer to account for the temporal sampling schedule of raven GPS locations and average GPS location error. In other words, if a raven location was within 100 m of an anthropogenic subsidy we considered the raven to have visited the subsidy feature immediately prior to, during, or immediately subsequent to the time the GPS location was recorded. Given that some of the GPS-fix schedules only recorded locations every 1–3 h, our calculations of visits to subsidies is a conservative estimate of actual visits. We only considered large-scale, high food density, and temporally consistent point-source subsidies, which were considered primary point-source subsidies. Naturally, there are numerous small-scale and ephemeral anthropogenic food subsidies that are utilized by ravens (e.g., litter and burn piles on private land). Therefore, the inference of the impact of anthropogenic subsidies on raven populations in this paper is conservative.

To measure space use with respect to anthropogenic subsidies, we calculated the proportion of locations from each bird-year-status that occurred at a highway/railroad or a point-source subsidy, separately. We used two generalized linear mixed models with the response variable being classified as a one if the location was within 100 m of a highway/railroad (highway/railroad model) or a point-source subsidy (point-source model) and a zero otherwise. Each model had a single fixed effect (breeding status) and a single random effect (bird-year). The random effect accounted for baseline within-individual correlations in the response variable (e.g., a nesting territory established adjacent to a highway) and unequal sample sizes among bird-years. We assumed a binomial distribution for the response with a logit-link function. Generalized linear mixed models were run using package lme4 in Program R (R Foundation for Statistical Computing, Vienna, Austria). We calculated Tukey comparisons among all breeding statuses using general linear hypothesis testing in the multcomp package. We also tested whether the proportion of a breeding raven's locations at a highway/railroad was related to distance of the nest from the nearest highway/railroad to

determine whether use of these features was either a behavioral (i.e., use not related to distance) or spatial process (i.e., use was related to distance). Finally, we tested whether raven nest success (i.e., successfully fledged ≥1 chick) was related to either distance from highway/railroad or the proportion of time the adult raven spent at highways/railroads (Webb et al. 2004).

Movement metrics and breeding status

We estimated simple movement behavior by calculating straight-line steplength (i.e., distance in m) between successive locations during the breeding season. To standardize steplengths across individuals with different location-recording schedules and missing fixes, we divided the steplength between successive locations by the number of hours between locations to yield per-hour steplength distances. We only calculated steplengths between successive locations that were within 48 h of each other (there were occasional gaps due to GPS-fix problems). Preliminary inspection showed that steplength distance was influenced by time of day, with ravens traveling longer distances during the middle of the day than in the morning, evening, or at night (Engel and Young 1992). We included a fixed quadratic effect to account for diurnal variation in steplengths. We centered time of day prior to generating the quadratic term. Our primary fixed effect of interest was breeding status, and we included a random intercept for bird-year to account for correlation in steplengths within individuals within each year across breeding status. Preliminary data exploration showed that the steplength data followed a lognormal distribution and as a result we set a Gaussian distribution with a log link. We excluded steplengths <50 m due to ARGOS satellite GPS location error that can result in a stationary GPS unit having an apparent steplength of ~18–47 m. Therefore, the steplength analysis only reflects distances traveled while moving, not activity levels per se (e.g., stationary raven locations on nests or roosts were excluded from this analysis). For the analysis, we used per-hour steplength distance as the response with three fixed-effect predictors (linear and quadratic time of day, breeding status) and one random-effect predictor (bird-year). We used lme4 for the full model and generated Tukey contrasts for all pairwise breeding status comparisons using multcomp.

Finally, we calculated a measure of general space use for each raven within each breeding status within each year. This metric was the average distance of GPS locations from the geographic center of all GPS locations for each raven-breeding-status-year. For example, the geographic center for breeding ravens was at or near the nest. For nonbreeding, post-failed nest, and post-successful nest, the geographic center was the center of all locations (not necessarily a place visited by the tagged raven). We chose this comparative metric because it provides a robust measure of the size of the landscape used by each raven within each breeding status (i.e., intensity of space use). It can be used to quantify whether, and how, ravens altered the intensity of their space use depending on whether they were breeding, post-successful nest, post-failed nest, or nonbreeding. We calculated average distance using the Standard Distance script within the Spatial Statistics Toolbox in ArcGIS Desktop 10.3.1 (ArcGIS 10.3; ESRI, Redlands, California, USA). Our statistical model had average distance as the response variable, breeding status as a fixed effect, and bird-year as a random effect to account for behavioral correlations within each bird within each year. All geographic calculations and data processing were done in ArcGIS Desktop 10.3.1 and QGIS 2.10.1 (QGIS Development Team 2004–2016, Open Source Geospatial Foundation Project, Chicago, Illinois, USA). All statistical analyses were conducted in Program R 3.2.2 (R Foundation for Statistical Computing).

Results

Twenty ravens were captured and GPS-tagged between 2012 and 2014. In 2012, nine ravens were tagged including three adult males, one subadult male, and five adult females. In 2013, seven ravens were tagged including five adult males and two adult females. In 2014, four ravens were tagged including two adult males and two adult females. In total, GPS-tagged birds included 10 adult males, nine adult females, and one subadult male.

Nest substrate

We located 35, 81, and 82 active raven nests in 2012, 2013, and 2014, respectively. Of these nests,

25 (5 in 2012, 10 in 2013, and 10 in 2014) were maintained by GPS-tagged ravens (Table 1). Considering all active nests within each year, the majority (96–100%) of raven nests were built on anthropogenic structures in all years (Table 1). Because all active nests represent nesting substrates that include nests that were active in multiple years, we also compared substrate category and types using only unique nest locations across years (i.e., each substrate structure only provides a single contribution to the calculations). Whether considering unique nest site locations within the nest census area or outside the census area, still <4% of nests were located on natural substrate (Table 2). Although nests were located on a wide variety of anthropogenic and natural substrates, the three most common nest substrates were as follows: oil/gas condensate tanks, barns and other buildings, and signs and billboards (Table 2).

Breeding status

Based on breeding season filter criteria defined in the *Methods* section, there were 26,147 raven GPS locations that were used in the breeding season space use and movement statistical analyses (Table 3). Based on the earliest start and latest end date of all individual breeding ravens within each year, the breeding season windows for 2012, 2013, and 2014 were defined as 30 March to 28 June, 14 March to 11 July, and 18 March to 25 July, respectively.

Table 1. Substrate types for all active common raven nests in south-central Wyoming, USA.

	GPS-tagged birds		Non-GPS birds		Total			
Year	Structure	Natural	Structure	Natural	Structure	Natural	Percentage of structure	Percentage of natural
2012	5	0	30	0	35	0	100.0	0.0
2013	9	1	69	2	78	3	96.3	3.7
2014	10	0	70	2	80	2	97.6	2.4
Grand total							97.7	2.3

Table 2. Specific substrate types for all unique (i.e., newly discovered) active common raven nests in south-central Wyoming, USA.

	Nest census area		Study area outside census area		Total	
Substrate category and nest substrate	No. of nests	%	No. of nests	%	No. of nests	%
Natural						
Cliff	1	1.9	0	0.0	1	0.7
Shrub/tree	1	1.9	1	1.1	2	1.3
Anthropogenic						
Abandoned equipment	1	1.9	2	2.1	3	2.0
Artificial nest platform	0	0.0	2	2.1	2	1.3
Barn/building	6	11.1	9	9.5	15	10.1
Bridge	2	3.7	1	1.1	3	2.0
Communication tower	2	3.7	1	1.1	3	2.0
Distribution power pole	0	0.0	1	1.1	1	0.7
Non-oil/gas-related tank	2	3.7	0	0.0	2	1.3
Oil/gas condensate tank	31	57.4	75	78.9	106	71.1
Phone-line pole	2	3.7	0	0.0	2	1.3
Railroad signal tower	1	1.9	0	0.0	1	0.7
Sign/billboard	3	5.6	3	3.2	6	4.0
Teepee	1	1.9	0	0.0	1	0.7
Windmill	1	1.9	0	0.0	1	0.7
Grand total	54		95		149	

Table 3. Sample sizes of GPS locations and ravens used in breeding season space use and movement analyses.

Breeding status	Total GPS locations	Individual ravens	Bird-years	Locations per bird-year		
				Min	Max	Average
Breeding	10,119	17	26	23	1346	389.2
Nonbreeding	9053	6	8	69	1942	1131.6
Post-failed	4288	7	7	259	1459	612.6
Post-successful	2687	9	14	53	806	191.9

Anthropogenic subsidies and space use

Across breeding statuses, the proportion of each bird-year's locations that were adjacent to highways or the railroad varied considerably, ranging from 0.00 to 0.69 with an average proportion of 0.14. Naïve breeding status-level proportions suggested that breeding birds spent significantly more time adjacent to a highway/railroad than other ravens in other breeding statuses. However, this naïve estimate failed to account for the fact that some breeding birds inherently spent more time near a highway/railroad because their nests were located adjacent to those features. After accounting for this baseline individual-level correlation, in the full model we found that breeding ravens still had the highest proportion of locations adjacent to a highway/railroad, followed by post-successful, nonbreeding, and post-failed ravens (Fig. 2). The difference in use of highways/railroad by ravens in different breeding statuses, though small, was statistically significant. Both post-successful and post-failed ravens used highways/railroad significantly less than breeding ravens, although the difference between nonbreeding and breeding ravens was not statistically significant. Interestingly, post-successful ravens used highways/railroad significantly more than post-failed ravens, such that post-successful ravens behaved more like breeding ravens than did post-failed ravens.

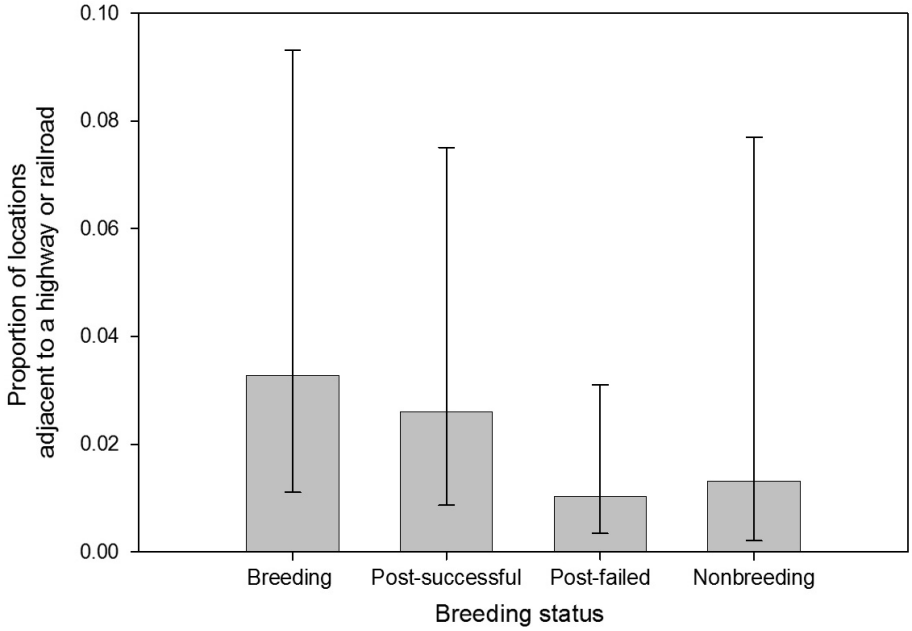

Fig. 2. Proportion of GPS locations occurring adjacent to a highway or railroad for each common raven breeding status from 2012 to 2014 in south-central Wyoming, USA. Breeding status estimates are model-adjusted to account for baseline correlation of space use patterns within individual bird-years. Error bars are 95% confidence intervals.

Nonbreeding ravens showed a wide variation in use of highway/railroad among individuals.

There was also high variability among individual ravens with respect to the proportion of locations at point-source subsidies, ranging from 0.00 to 0.56 with an across-breeding status average of 0.06. Naïve estimates of point-source subsidy space use suggested that breeding ravens used these features significantly less than all other breeding statuses. After incorporating a baseline factor to account for individual-level behavioral patterns, the apparent difference in use of point-source subsidies became even more pronounced (Fig. 3). Breeding and post-successful ravens had nearly zero visits to point-source subsidies (<0.1% of locations, on average), whereas post-failed and especially nonbreeding birds visited these features more often (1.3% and 12.5% of locations, respectively, and on average). All pairwise differences among breeding statuses in Fig. 3 are statistically significant (all $P < 0.006$), with the exception of post-failed ravens, which did not show statistically different rates of visiting point-source subsidies than nonbreeding ravens ($P = 0.255$). Post-failed ravens visited point-source subsidies 16.7 times more often than post-successful ravens (1.25% ÷ 0.075% = 16.7; $P = 0.006$). The wide confidence interval (CI) on nonbreeding ravens indicates that while, on average, nonbreeding ravens visited point-source subsidies often, there was substantial variation in visitation rates among nonbreeding ravens (i.e., some nonbreeding ravens never visited point-source subsidies during the breeding season; range in proportion of nonbreeding locations at subsidies by bird-year = 0.00–0.43).

There was a clear break in the distance of nests of GPS-tagged ravens from the nearest highway/railroad. Twelve of the nests were within 400 m, and the remaining 14 nests were >2360 m from the nearest highway/railroad. For the 12 nests within 400 m, we found that the frequency with which those ravens visited a highway or railroad was strongly correlated with the distance of the nest from the highway/railroad (Fig. 4). For every 100 m farther from the nearest highway/railroad, the proportion of breeding raven locations adjacent to a highway/railroad declined by

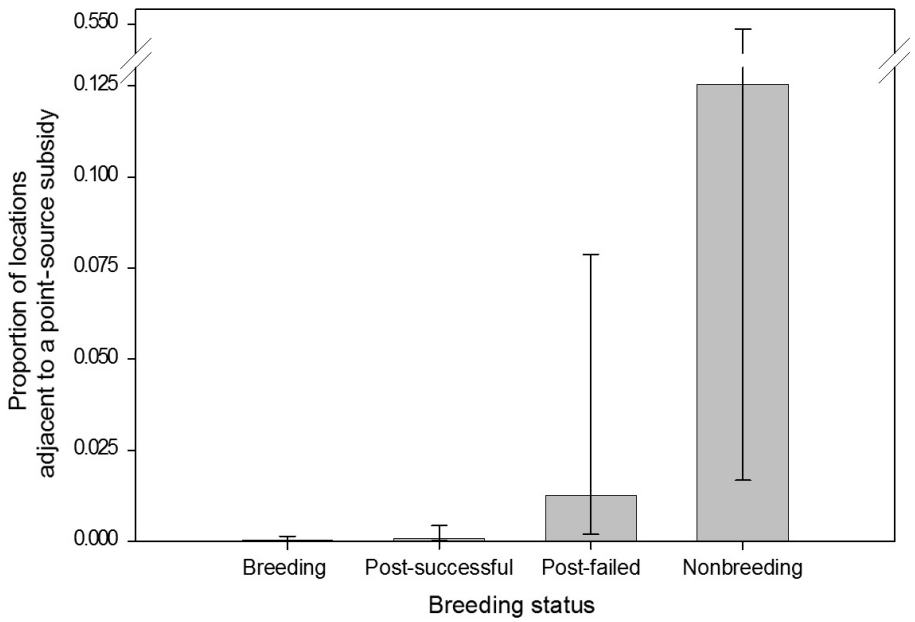

Fig. 3. Proportion of GPS locations occurring adjacent to a point-source subsidy (e.g., landfill) for each common raven breeding status from 2012 to 2014 in south-central Wyoming, USA. Breeding status estimates are model-adjusted to account for baseline correlation of space use patterns within individual bird-years. Error bars are 95% confidence intervals (CIs). *Y*-axis has a range break to facilitate among-breeding status comparisons given wide CI on nonbreeding visitation rates.

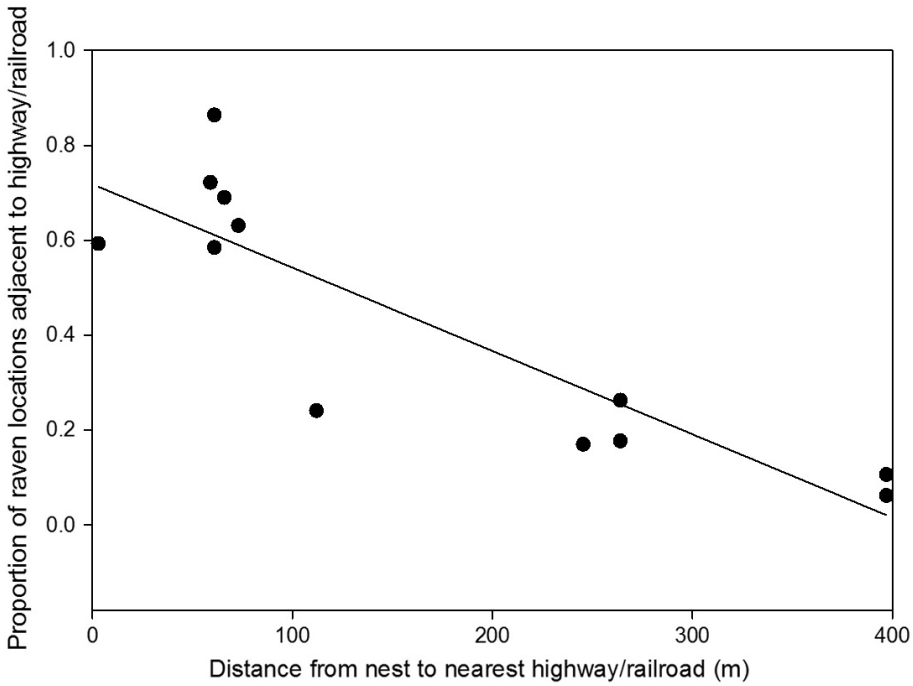

Fig. 4. Proportion of breeding raven locations adjacent to a highway or railroad as a function of distance from the nest to the nearest highway/railroad. Regression line only calculated for nests within 400 m of a highway or railroad. All excluded GPS-tagged raven nests were >2360 m from the nearest highway/railroad.

0.176 (R^2 = 0.76, P < 0.001). However, nest fate (i.e., successful vs. failed) was not related to distance from the nearest highway/railroad (P = 0.516) or the proportion of a raven's locations that were adjacent to a highway/railroad (P = 0.408). For nests >2360 m from the nearest highway/railroad, the average proportion of each raven's GPS locations at a highway or railroad was 0.0038 (range: 0.000–0.031).

Movement metrics and breeding status

There was a statistically significant diurnal quadratic trend in steplengths, with short/zero steplengths at night and longest steplengths (avg. = ~1400 m/h) during the afternoon (centered time, β1 = −0.076, β2 = −0.018, P < 0.001). This diurnal trend is model-adjusted to account for baseline differences in steplengths among breeding statuses and for behavioral patterns within individual ravens (Fig. 5).

After accounting for the temporal shift in average steplengths, and after accounting for the baseline behavioral patterns and correlation within individual bird-years, ravens showed differences in movement rates as a function of breeding status. Specifically, breeding ravens traveled the shortest steplength rates (695.2 m/h, 95% CI: 524.2–921.9), followed by post-successful (847.9 m/h, 95% CI: 615.9–1167.3) and then post-failed ravens (1357.0 m/h, 95% CI: 928.7–1982.8). Nonbreeding ravens traveled the farthest steplength rates when moving (2783.0 m/h, 95% CI: 1701.0–4553.5). Pairwise comparisons showed that nonbreeding ravens traveled significantly further than both breeding (diff = 2087.8 m/h, P < 0.001) and post-successful ravens (diff = 1935.1 m/h, P < 0.001). Post-failed ravens also traveled significantly farther than breeding ravens (diff = 661.8 m/h, P < 0.001). Post-failed ravens movement distances were not statistically different from nonbreeding ravens (diff = 1426.0 m/h, P = 0.0924) or post-successful ravens (diff = 509.1 m/h, P = 0.0733), and post-successful ravens were not statistically different from breeding ravens (diff = 152.7 m/h, P = 0.1489).

The average distance of a raven from the geographic center of its activity area during the breeding season was strongly related to breeding

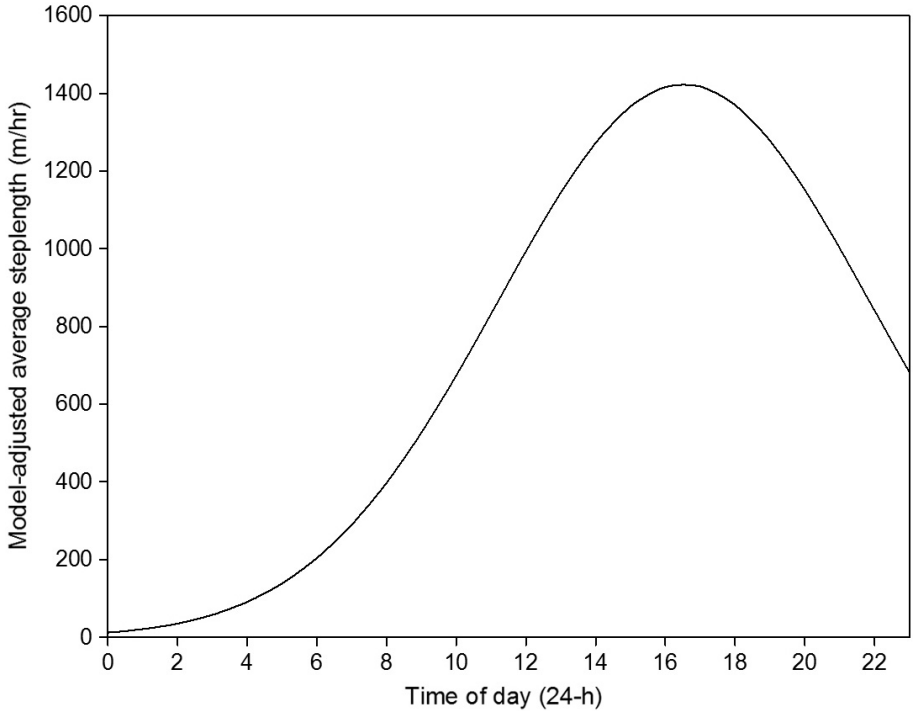

Fig. 5. Average steplength (m/h) of moving common ravens throughout the 24-h period. Stationary raven locations were excluded from analysis. Steplength distances are model-adjusted to account for individual raven correlation and behavioral patterns and baseline differences among breeding statuses.

status (Fig. 6). When off the nest, breeding ravens were an average of 0.8 km (95% CI: 0.5–1.3 km) from the nest. Ravens that were not actively attending a nest had significantly higher average location distances than breeding ravens, including post-successful (0.3 km farther, $P = 0.001$; mean distance 1.1 km, 95% CI: 0.6–1.9), post-failed (8.6 km farther, $P < 0.001$; mean distance 9.4 km, 95% CI: 5.4–16.7), and nonbreeding ravens (9.6 km farther, $P < 0.001$; mean distance 10.4 km, 95% CI: 4.1–26.3). Additionally, post-failed ravens ranged over significantly greater distances than post-successful ravens (8.6 times farther, 95% CI: 5.6–13.3, $P < 0.001$), yet post-failed ravens did not range across the landscape different than nonbreeding ravens (0.9 times as far, 95% CI: 0.3–2.7, $P = 0.998$).

Discussion

Our primary goal was to determine how primary anthropogenic subsidies benefit common raven populations with a particular focus on the breeding season. Our secondary goal was to measure how ravens used two-dimensional space during the breeding season and whether space use differed depending on breeding status. Overwhelmingly, we found that raven nests were built on anthropogenic structures. Breeding ravens frequently visited highways and railroads, although their visitation rates were directly and inversely proportional to the distance between the nest and the nearest highway/railroad. Nonbreeding ravens, but not breeding ravens, regularly visited point-source subsidies, such as landfills and transfer stations. Both breeding ravens and ravens who had successfully raised chicks to fledging (post-successful) used small, defined portions of the landscape, whereas nonbreeding ravens and ravens who had failed nests (post-failed) ranged widely. The take-home findings are as follows: (1) breeding ravens built nests on anthropogenic structures and subsequently used small portions of the landscape intensively; (2) nonbreeding ravens frequently visited point-source subsidies; (3)

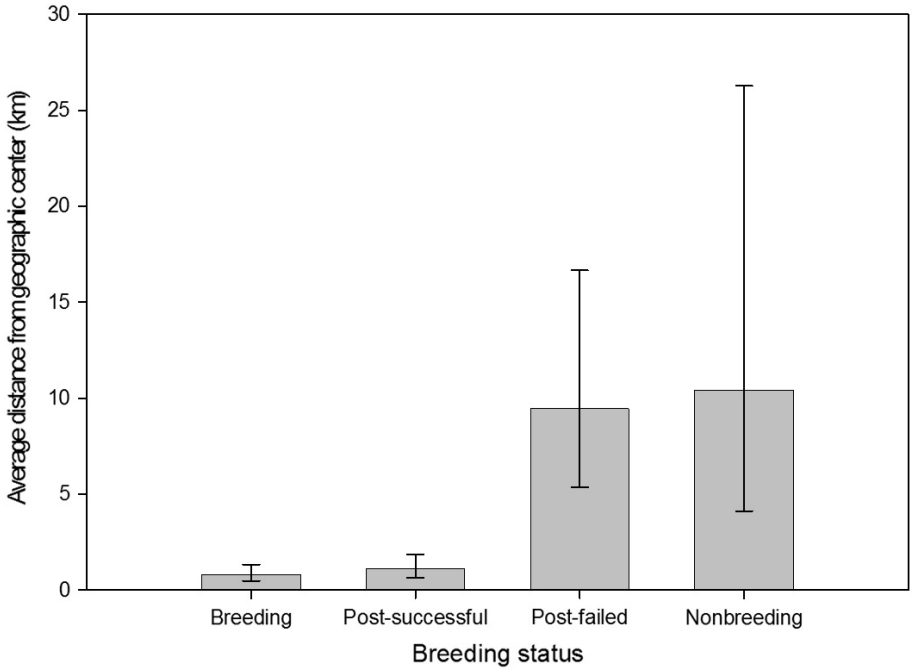

Fig. 6. Average distance of a common raven location from the geographic center of all of its locations within a breeding status within each year. Geographic center for breeding birds is the active nest. Error bars are 95% confidence intervals.

nonbreeding ravens used large swathes of the landscape sparsely; and (4) post-nesting ravens with failed nests used the landscape and anthropogenic food subsidies similar to nonbreeding ravens, whereas post-nesting ravens with successful nests behaved similar to breeding ravens.

Nest substrate

We found that common raven nests were overwhelmingly built on anthropogenic structures. Whether considering all active nests annually or only counting each individual nest substrate one time across years, the proportion of nests that were on anthropogenic vs. natural substrates ranged from 96% to 100% among years. This is similar to findings from other studies on raven nesting substrate in sagebrush-steppe, which have found that 75–80% of active raven nests were built on anthropogenic structures (Coates et al. 2014, Howe et al. 2014). This is one of the mechanisms by which raven populations are subsidized. There are few natural elevated structures in sagebrush-steppe on which ravens can build nests (e.g., cliffs, rock outcrops, or trees; Boarman and Heinrich 1999), especially in our study area. Once humans build anthropogenic structures, these structures are rapidly utilized by nest-building ravens (Steenhof et al. 1993). We did not quantify the magnitude that the anthropogenic substrates subsidized raven nesting because of the difficulty in determining where and at what densities they might have nested at in the absence of the anthropogenic features. Rather, we suggest that the mere fact that ravens overwhelmingly chose to build nests on anthropogenic features represents some unquantified level of subsidy, ranging from relatively minor (e.g., greater perceived substrate stability than adjacent natural substrates), to relatively major (e.g., anchoring a breeding raven pair in the sagebrush-steppe where otherwise no ravens would have nested due to the absence of natural substrates).

Anthropogenic subsidies and space use

Breeding ravens visited highways and railroads more often than ravens in other breeding statuses. This difference was present even after

statistically accounting for the fact that some ravens had high highway/railroad visitation rates simply because their nests were adjacent to a highway or railroad. Over half of GPS-tagged ravens (53.8%) occupied nests that were >2360 m from the nearest highway or railroad, but the remaining 46.2% of raven nests were all within 400 m of the nearest highway or railroad. This suggests that some ravens were preferentially occupying nests adjacent to highways/railroads, likely to facilitate access to road-killed birds and mammals (Kristan et al. 2004). However, we also found that for those 46.2% of raven nests adjacent to a highway or railroad, the GPS-tagged ravens' actual use of these features was strongly related to the feature's distance from the nest. This suggests that ravens are not preferentially scavenging along highways and railroads, but rather that they will opportunistically use these features to the extent that they are encountered in regular scavenging activities (Kristan and Boarman 2007). Kristan et al. (2004) found that all breeding ravens foraged near their nests, and when the nests happened to occur near roads, the ravens also foraged opportunistically along the roadway. This is likely a function of central place foraging around the nest, whereby raven foraging intensity decreases with increasing distance from the nest (Rösner and Selva 2005). Unlike previous raven studies in the Mojave desert (Kristan and Boarman 2007), our study did not find increased nest success with shorter distance from the nearest highway or railroad.

Nonbreeding ravens frequently visited point-source subsidies and did so significantly more often than post-failed ravens (12.5% vs. 1.2% of each individual's locations) or post-successful and breeding ravens, which rarely visited point-source subsidies (0.1% and 0.0%, respectively). This is likely explained by previous findings that breeding ravens forage intensively in the area surrounding their nest (Kristan et al. 2004, Rösner and Selva 2005), whereas nonbreeding ravens can adapt flexible space use patterns to take advantage of anthropogenic food sources over large areas (Heinrich et al. 1994, Webb et al. 2012, Loretto et al. 2015). It is likely that breeding ravens would take advantage of point-source subsidies (Kristan et al. 2004, Roth et al. 2004, Kristan and Boarman 2007), but only when their nests were already close to those subsidies (Kristan et al. 2004). It is possible that our sample of ravens rarely/never occurred at point-source subsidies simply because all nests were too far away (range 5300–13,900 m) from the nearest point-source subsidy. There are also numerous small or ephemeral point-source subsidies that ravens utilize that we were unable to capture in this study. Regardless, our results indicate that nonbreeding ravens, but not breeding ravens, will travel widely to utilize point-source subsidies.

We note that other anthropogenic subsidies that were not quantified in this study certainly benefit both breeding and nonbreeding ravens. For example, ephemeral food sources or roosting/perching structures are frequently used by ravens. Thus, we condition our inference on the impact and physical use, as a function of breeding status, of the primary anthropogenic subsidies that we included in this analysis.

Movement metrics and breeding status

When moving (i.e., not roosting), nonbreeding ravens traveled the greatest distances among breeding classes (average ≈ 2800 m/h) and ranged over the largest areas (average distance from range center ≈ 10.4 km), followed by post-failed and post-successful ravens. Breeding ravens traveled the shortest distances when moving (average ≈ 700 m/h) and only ranged over small portions of the landscape surrounding the nest (average distance from range center ≈ 0.8 km). These findings are consistent with previous studies, which also found that breeding ravens focus the majority of their activity in the area surrounding the nest (Kristan et al. 2004, Rösner and Selva 2005, Marzluff and Neatherlin 2006), whereas nonbreeding ravens move widely (Marzluff and Neatherlin 2006, Webb et al. 2012).

Raven impacts on greater sage-grouse

While we did not directly quantify raven impacts on nesting sage-grouse, we can make some inferences in the context of previous research. Other studies have found variable effectiveness of lethal raven control on improving sage-grouse nesting success that could be explained by the results we present here. Coates (2007) found that sage-grouse nest success was

improved along lethal raven control routes in Nevada (but not at sage-grouse nests far from roads), and Manzer and Hannon (2005) found that sage-grouse nest success was 8× higher in landscapes with lower corvid density. Bui et al. (2010) found that in sagebrush-steppe in Wyoming the presence of ravens, not raven abundance, was negatively related with sage-grouse nest success. In contrast, Dinkins et al. (2016) found that lethal raven control of transient nonbreeding ravens at point-source subsidies was associated with improved sage-grouse nest success in Wyoming after accounting for temporal interactions, weather influences, and coyote control. Our results agree with previous studies that suggest that raven control at point-source subsidies during the breeding season will not impact breeding ravens, which forage intensively in sagebrush-steppe around their nest and consequently can cause high rates of sage-grouse nest depredation. In landscapes where nonbreeding ravens travel widely and encounter sage-grouse nests, lethal raven removal at point-source subsidies may contribute to improved landscape-level sage-grouse nest success (Dinkins et al. 2016). Inducing raven nest failure (i.e., mimicking our findings here from natural nest failures) may be a useful tool to switch breeding raven behaviors to those of nonbreeding ravens, the lethal control of which has shown some effectiveness at increasing sage-grouse nest success (Coates 2007, Dinkins et al. 2016).

Management Implications

We identified two main sources of anthropogenic sources of subsidies to breeding and nonbreeding ravens. First, breeding ravens built nests almost exclusively on anthropogenic structures, including oil and gas facilities, abandoned buildings, and billboards. In sagebrush-steppe where natural elevated features are rare, anthropogenic structures appear to be a major feature allowing ravens to breed (or roost) in portions of the landscape that would be otherwise inaccessible. Second, point-source food subsidies (e.g., landfills and transfer stations) were frequently used by nonbreeding, and to a lesser extent, post-failed ravens. These ravens ranged extensively, and consequently, the subsidy of the point source to the raven population extended beyond the spatial extent of the point features. We found that highways and railroads, while used more often by breeding ravens than ravens in other breeding statuses, were used directly proportional to the distance from the nest to the highway/railroad and were used opportunistically. Highways and railroads therefore served as a minor subsidy to breeding ravens, specifically to those whose nests were adjacent to these linear features.

Movement and space use analyses showed that breeding ravens occupied small portions of the landscape around their nest, whereas nonbreeding ravens traveled long distances and ranged widely. With respect to greater sage-grouse, we hypothesize that breeding ravens have a higher impact on sage-grouse nest success because of their intense use of small portions of the landscape. When sage-grouse nest within a breeding raven territory, the ravens are more likely to detect and depredate the sage-grouse nest. Therefore, the subsidization of nesting substrate is compounded by the space use behavior of breeding ravens. In contrast, nonbreeding ravens may have a much lower probability of encountering sage-grouse nests because of their sparse use of any particular portion of the landscape and their frequent use of point-source subsidies. Ravens that had failed nests switched to a blend of movement and space use between that of breeding and nonbreeding ravens, concomitantly reducing their energy demands and their likelihood of encountering and depredating sage-grouse nests. Post-breeding ravens with successful nests continued to move and use space like breeding ravens (due to continued care for fledged young) and still would be expected to have higher energy demands and sage-grouse nest encounter rates.

Causing nest failure may induce territorial ravens to switch to a wider-ranging nonbreeding raven space use pattern, reducing the localized impact of breeding ravens on sage-grouse nest success, and rendering those ravens vulnerable to lethal control actions at point subsidies.

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Literature Cited

Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. https://birdsna.org/Species-Account/bna/species/476/articles/introduction

Bui, T., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65–78.

Coates, P. S. 2007. Greater sage-grouse (*Centrocercus urophasianus*) nest predation and incubation behavior. Dissertation. Idaho State University, Pocatello, Idaho, USA.

Coates, P. S., J. W. Connelly, and D. J. Delehanty. 2008. Predators of greater sage-grouse nests identified by video monitoring. Journal of Field Ornithology 79:421–428.

Coates, P. S., K. B. Howe, M. L. Casazza, and D. J. Delehanty. 2014. Landscape alterations influence differential habitat use of nesting buteos and ravens within sagebrush ecosystem: implications for transmission line development. Condor 116:341–356.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Dinkins, J. B., M. R. Conover, C. P. Kirol, J. L. Beck, and S. N. Frey. 2016. Effects of common raven and coyote removal and temporal variation in climate on greater sage-grouse nesting success. Biological Conservation 202:50–58.

Dunk, J. R., R. N. Smith, and S. L. Cain. 1997. Nest-site selection and reproductive success in common ravens. Auk 114:116–120.

Engel, K. A., and L. S. Young. 1992. Daily and seasonal activity patterns of common ravens in southwestern Idaho. Wilson Bulletin 104:462–471.

Heinrich, B., D. Kaye, T. Knight, and K. Schaumburg. 1994. Dispersal and association among common ravens. Condor 96:545–551.

Howe, K. B., and P. S. Coates. 2015. Observation of territorial breeding common ravens caching eggs of greater sage-grouse. Journal of Fish and Wildlife Management 6:187–190.

Howe, K. B., P. S. Coates, and D. J. Delehanty. 2014. Selection of anthropogenic features and vegetation characteristics by nesting common ravens in the sagebrush ecosystem. Condor 116:35–49.

Kelly, J. P., K. L. Etienne, and J. E. Roth. 2005. Factors influencing the nest predatory behaviors of common ravens in heronries. Condor 107:402–415.

Kristan III, W. B., and W. I. Boarman. 2007. Effects of anthropogenic developments on common raven nesting biology in the West Mojave Desert. Ecological Applications 17:1703–1713.

Kristan III, W. B., W. I. Boarman, and J. J. Crayon. 2004. Diet composition of common ravens across the urban-wildland interface of the West Mojave Desert. Wildlife Society Bulletin 32:244–253.

Lockyer, Z. B., P. S. Coates, M. L. Casazza, S. Espinosa, and D. J. Delehanty. 2013. Greater sage-grouse nest predators in the Virginia Mountains of northwestern Nevada. Journal of Fish and Wildlife Management 4:242–254.

Loretto, M. C., S. Reimann, R. Schuster, D. M. Graulich, and T. Bugnyar. 2015. Shared space, individually used: spatial behavior of non-breeding ravens (*Corvus corax*) close to a permanent anthropogenic food source. Journal of Ornithology. https://doi.org/10.1007/s10336-015-1289-z

Manzer, D. L., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multiscale approach. Journal of Wildlife Management 69:110–123.

Marzluff, J. M., and E. Neatherlin. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. Biological Conservation 130:301–314.

Moynahan, B. J., M. S. Lindberg, J. L. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. Journal of Wildlife Management 71:1773–1783.

Peebles, L. W., M. R. Conover, and J. B. Dinkins. 2017. Adult sage-grouse numbers rise following raven removal or an increase in precipitation. Wildlife Society Bulletin 41:471–478.

Rösner, S., and N. Selva. 2005. Use of the bait-marking method to estimate the territory size of scavenging birds: a case study on ravens *Corvus corax*. Wildlife Biology 11:183–191.

Roth, J. E., J. P. Kelly, W. J. Sydeman, and M. A. Colwell. 2004. Sex differences in space use of breeding common ravens in western Marin County, California. Condor 106:529–539.

Sauer, J. R., and W. A. Link. 2011. Analysis of the North American Breeding Bird Survey using hierarchical models. Auk 128:87–98.

State of Wyoming. 2015. Office of Governor Mead. State of Wyoming Executive Department Executive Order. Greater Sage Grouse Area Protection. 2015–04.

Steenhof, K., M. N. Kochert, and J. A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. Journal of Wildlife Management 57:271–281.

Stiehl, R. B. 1985. Brood chronology of the common raven. Wilson Bulletin 97:78–87.

Stiehl, R. B., and S. N. Trautwein. 1991. Variations in diets of nesting common ravens. Wilson Bulletin 103:83–92.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336–347.

USFWS [US Fish and Wildlife Service]. 2008. Initiation of status review for the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 73:10218–10219.

USFWS. 2010. 12-Month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 75:13910–14014.

USFWS. 2015. 12-Month finding on a petition to list greater sage-grouse (*Centrocercus urophasianus*) as an endangered or threatened species. Federal Register 80:59858–59942.

Webb, W. C., W. I. Boarman, and J. T. Rotenberry. 2004. Common raven juvenile survival in a human-augmented landscape. Condor 106:517–528.

Webb, W. C., J. M. Marzluff, and J. Hepinstall-Cymerman. 2012. Differences in space use by common ravens in relation to sex, breeding status, and kinship. Condor 114:584–594.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters 6:996–1003.