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RESEARCH ARTICLE



Isotopic analysis reveals landscape patterns in the diet of a subsidized predator, the common raven

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Abstract

- 1. Anthropogenic subsidies to native predators can have cascading effects on sensitive prey populations, but the spatial mechanisms behind these effects are often unknown.
- 2. We used a stable isotope mixing model to reconstruct spatially naïve assimilated diets of common raven (Corvus corax) chicks and then used regression analysis to investigate landscape patterns in assimilated chick diet, with particular respect to the eggs and chicks of greater sage-grouse (Centrocercus urophasianus).
- 3. Assimilated raven diets were primarily composed of mammal carrion, followed by anthropogenic food and sage-grouse eggs and chicks.
- 4. Raven diets showed landscape gradients, whereby raven chicks in nests near active greater sage-grouse breeding leks consumed a higher proportion of sage-grouse eggs, sage-grouse chicks and insects in their diet and less mammal carrion. A majority of raven nests on anthropogenic nesting structures (78.7%) were within 5 km of the nearest sage-grouse lek. Ravens nesting in high-probability greater sage-grouse nesting habitat consumed more insects and plants and less mammal carrion.
- 5. In landscapes devoid of natural raven nesting substrates, such as our study area, anthropogenic nesting substrates can 'anchor' breeding ravens nearer to greater sage-grouse leks, with concomitant increases in raven predation on greater sagegrouse nests. Curtailment of anthropogenic nesting substrates within 5 km of a sage-grouse lek may have a disproportionately positive impact on sage-grouse populations. More generally, these findings highlight that the spatial arrangement of anthropogenic subsidies can result in indirect interactions between humans and predators with direct implications for predators and prey.

KEYWORDS

Centrocercus urophasianus, common raven, Corvus corax, diet analysis, greater sage-grouse, landscape patterns, stable isotopes, subsidized predator

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1 | INTRODUCTION

Common ravens (Corvus corax) are a native generalist avian predator widespread across North America and Eurasia. In the western United States, raven populations have increased dramatically over the past 50 years (Sauer & Link, 2011). Concomitant with range expansion and increases in abundance, humans inadvertently subsidize raven populations via garbage, road-killed carrion, artificial nesting substrates and reduction of native predators and competitors (Boarman et al., 2006; Brockman et al., 2019; Harju et al., 2018; Kristan & Boarman, 2007; O'Neil et al., 2018; Steenhof et al., 1993; Wilmers et al., 2003). Of particular note here is the anthropogenic subsidy of artificial nesting substrates. In much of western North America, including the sagebrush steppe and Mojave Desert, natural substrates are limited. Decades of agriculture, ranching and energy development in western North America have resulted in numerous anthropogenic structures that serve as artificial nesting substrates for ravens, 'anchoring' them to landscapes in which they would have not previously bred (Harju et al., 2018; Howe et al., 2014; Kristan & Boarman, 2007; Roth et al., 2004). During the breeding period, ravens forage almost exclusively near the nest, on average within 800 m of the nest (Harju et al., 2018; Rösner & Selva, 2005; Roth et al., 2004). The anchoring function of the nest predictably leads to spatial variation in raven diets (Stiehl & Trautwein, 1991). Nests close to point subsidies (e.g. landfills) have a high amount of trash in their diet, ravens nesting near roads have a high amount of carrion in their diet and ravens far from both roads and point subsidies eat more native diet items (Kristan et al., 2004). Thus, if anchored in landscapes via artificial nesting substrates, ravens may alter their diets by foraging for prey and diet items surrounding the nest (Harju et al., 2018).

Greater sage-grouse (hereafter, sage-grouse; Centrocercus urophasianus) occur across large swaths of the western United States, particularly tied to the sagebrush steppe ecosystem. Sagegrouse populations have declined 17%-47% from historic levels and occupied range has been reduced by approximately 44% over the past several decades (Connelly & Braun, 1997; Schroeder et al., 2004). Ravens are known to impact sage-grouse at the population level via raven depredation of sage-grouse nests and young (Coates et al., 2008; Coates et al., 2020; Conover & Roberts, 2017; Dinkins et al., 2016; Peebles et al., 2017; Taylor et al., 2012; Taylor et al., 2017). Predation can account for as much as 82.5%-94.0% of sage-grouse nest failures (Lockyer et al., 2013; Moynahan et al., 2007), and ravens specifically have been documented preying on and destroying 46.7%-58.8% of monitored sage-grouse nests (Coates et al., 2008; Lockyer et al., 2013). Sage-grouse often nest at higher densities near communal breeding leks, which are flat, open areas where males and females congregate to display and breed prior to female nest initiation off of the lek.

Use of anthropogenic structures for nesting (Figure 1) may result in increased raven predation on sage-grouse in the surrounding area. In much of the sagebrush steppe, natural nesting substrates (e.g. cliffs and trees) are rare (Coates et al., 2014). In these areas, ravens will frequently nest on transmission lines, buildings, bridges, oil and gas infras-



FIGURE 1 Common raven nest in an abandoned trailer, highlighting the lack of natural nesting substrates within the study area, southcentral Wyoming, USA, 2013–2014

tructure and other anthropogenic features (Coates et al., 2014; Harju et al., 2018; Howe et al., 2014; Steenhof et al., 1993). This effectively results in an anthropogenic subsidy, whereby breeding ravens with high energy demands and intensive foraging around the nest are anchored in sage-grouse nesting habitat. To date, no known study has investigated whether, as a result of anchoring, there is spatial variation in assimilated raven diets that can be tied to predation on sage-grouse eggs and chicks.

We sought to understand the spatial patterns of dietary composition of a subsidized raven population with respect to sage-grouse using stable isotope analysis of the ratios of carbon and nitrogen (Ben-David et al., 1997; Kelly, 2000; Scholz et al., 2020). Because breeding raven pairs forage almost exclusively within ~0.8-2 km of the nest (Harju et al., 2018; Rösner & Selva, 2005, S. Harju unpublished data), and because isotope ratios within tissues are fixed at the time of tissue creation (Phillips, 2012), raven chick feathers provide a definitive isotopic timestamp of adult raven foraging patterns during the reproductive window between egg formation and chick fledging. In this study, we partitioned dietary contributions of local potential general diet items to raven chick diets. We then placed these non-spatial dietary composition results into a spatially explicit landscape regression model, with the ultimate goal of identifying general landscape patterns in raven foraging and the potential effects it could have on sage-grouse.

2 | MATERIALS AND METHODS

2.1 Study area

Our study area encompassed approximately 3200 km² in southcentral Wyoming (Figure 2). The habitat was flat to moderately rolling sage-steppe vegetation communities including abundant sage-grouse nesting habitat (Dzialak et al., 2013). The region has undergone extensive energy development resulting in anthropogenic features across the landscape such as highways, improved gravel roads, well pads,



FIGURE 2 Map depicting raven chick nests sampled relative to highways, garbage dumps and transfer stations within the range of greater sage-grouse in southcentral Wyoming, USA, 2013–2014. There were >150 active sage-grouse leks within the extent of the main panel at the time of the study; however, lek locations are not shown due to conservation concerns

overhead transmission power lines, communication towers, abandoned structures and solid waste dumps and transfer stations. Within the study area, energy development was extensive in the southern portion declining to non-existent in the north. Grazing by cattle and sheep was prominent throughout the study area and most water sources, albeit limited but evenly distributed, were related to livestock in the forms of anthropogenic water wells, cattle tanks and cattle ponds. To quantify nesting substrates, we conducted exhaustive field searches of active raven nests within the study area to assess nesting substrate, regardless of whether the nest was accessible for stable isotope sampling. The study area had an extensive road network and potential nesting substrates were easily identified and searched.

2.2 | Stable isotope sampling

Feathers are keratinized tissues that preserve the isotopic record indefinitely and can represent data spanning the period for which the feathers were grown (Pearson et al., 2003). We collected and combined two scapular feathers from 179 raven nestlings (usually two nestlings per nest) via clipping for stable isotope analysis of carbon (δ^{13} C) and nitrogen (δ^{15} N). Feathers were collected between 9 May and 3 July in 2013 and 2 May and 17 July in 2014. Only fully-grown or emerged portions of pin feathers were collected (i.e. dry feathers only) and clippings measured approximately 50 mm on average but varied depending on the age of chicks and stage of feather development. Feathers were placed in individually labelled and sealed paper envelopes and stored at room temperature until shipment to the analytical lab. The sampling was non-lethal and minimally invasive. All raven chicks from which feathers were collected were banded with U.S. Fish and Wildlife Service (USFWS) leg bands and returned to the nest (Federal Bird Banding Permit #23780).

We also collected samples from potential diet items within the study area. These items included hair samples collected from opportunistic road-killed herbivore mammals (n = 6; three domestic cows [Bos taurus], one domestic sheep [Ovis aries], one jackrabbit [Lepus townsendii] and one pronghorn [Antilocapra americana]), greater sage-grouse egg shell membranes from already hatched or depredated nests (n = 13), sage-grouse feathers from already hatched or depredated nests (n = 5) and sage-grouse feathers from a depredated hen (n = 1) found within the study area. We also collected anonymous human hair samples that were pooled from floors of hair salons and barber shops in Rawlins, Wyoming. These human hair samples were used to generally reflect composite anthropogenic diets (e.g. composite isotopic signatures of anthropogenic food sources such as dumps and transfer stations often based on C₄ plants; O'Connell & Hedges, 1999). All samples were stored in individually labelled paper envelops and sent to the analytical lab for analysis.

2.3 | Laboratory analysis

All samples were sent to the University of Wyoming Stable Isotope Facility (Laramie, Wyoming, USA) for sample preparation and analysis following each field season. To clean the samples, a 2:1 mixture of chloroform:methanol was used to rinse each sample, followed by three rinses of deionized water. Samples were loaded into tins with a range from 0.75 to 0.85 mg. The standard uncertainty for the lab's instruments for carbon is 0.15 permil and for nitrogen is 0.2 permil, although the precision was less than or equal to 0.1 permil for all runs of our samples. Samples were ground into extremely fine powder using a ball mill. Isotopic analyses were conducted using a Carlo Erba 1110 or Costech 4010 Elemental Analyzer coupled to a Finnigan Delta+XP continuous flow inlet isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany). Repeated measurements with laboratory CO₂-in-air working standards had a precision of <0.1%. The δ^{13} C values of CO₂ in respiration samples were corrected to the international standards, Vienna Pee Dee Belemnite for ¹³C and the atmospheric nitrogen for ¹⁵N. We calculated δ values (per mil, ∞) using

$$\delta X = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right],$$

where X is the element of interest (¹³C or ¹⁵N), R_{sample} is for the ratio of the heavier to lighter isotope (¹³C/¹²C or ¹⁵N/¹⁴N) of the sample, and $R_{standard}$ is for the ratio (¹³C/¹²C or ¹⁵N/¹⁴N) of the international standard. Reporting of isotope data and measurement results follow the guidelines provided by Coplen (2011).

2.3.1 | Tissue and fractionation adjustments

We post-processed laboratory results of the source diet item in two ways. First, we combined mammals into a single 'mammal carrion' category because: (1) we lacked sufficient species-specific sample sizes to estimate diet contribution of each mammal species, (2) all mammals shared similar ecological niches compared to other potential diet sources and (3) ravens likely feed on mammal carcasses opportunistically. We did not consider mammalian predators as potential diet items because Kristan et al. (2004) found evidence of predators in only 0.2% of raven pellets. Second, we used data from the peer-reviewed literature to adjust the stable isotope values from our tissue samples to reflect fractionation within the body of each source species. We did this because adult ravens were likely bringing energy-rich tissues (e.g. muscle) of mammals to the nest rather than our sampled tissue (e.g. fur). We subtracted 1.6% from the δ^{13} C value for all mammal fur samples to reflect mammal muscle (hereafter 'mammal carrion'; Caut et al., 2009; Roth & Hobson, 2000). We subtracted 4.15% from the δ^{15} N value and subtracted 1.85% from the δ^{13} C value for all human hair samples to reflect human diet in the study area (hereafter 'anthropogenic food'; Minagawa, 1992; Schoeller, 1986). We subtracted 3.41% from the δ^{13} C value for all sage-grouse egg membranes to reflect egg yolk and albumen but did not adjust the δ^{15} N values for eggs (Hobson, 1995). We subtracted 2.14‰ from the δ^{15} N value and 1.24‰ from the δ^{13} C

value for all sage-grouse feather samples to reflect sage-grouse muscle (hereafter 'sage-grouse chick'). We used previously published data from the literature to define the isotopic values of sagebrush steppe C₃ plants ($\delta^{15}N = 1.54\%$, $\delta^{13}C = -26.60\%$; Feranec, 2007; Kelly, 2000; Kohn, 2010; Mowat & Heard, 2006) and sagebrush steppe insects during spring ($\delta^{15}N = 5.65\%$, $\delta^{13}C = -25.51\%$; Blomberg et al., 2013).

2.4 | Statistical analysis of diet composition

We used MixSIAR (v. 3.0.2) to build a source partitioning Bayesian mixing model (https://github.com/brianstock/MixSIAR/releases). Input data were tissue-adjusted means and *SD* for field-sampled diet items and literature-derived data for plants and insects. We used lab experiment data from Hobson and Clark (1992) and Newsome et al. (2015) to specify source-to-juvenile-corvid feather fractionation rates separately for each diet item (Table S1).

In MixSIAR, we set year as a fixed effect and nest as a random effect nested within year to account for sampling two chicks per nest for most nests. We set a residual*process error structure meaning the consumer population is neither assumed to be a perfect specialist nor generalist but can rather fall somewhere in between (Stock & Semmens, 2016). We used a Dirichlet prior on the global estimated proportions because diet item proportions are not independent (i.e. they must sum to 1.0), which in practice assigned equal-weight prior probabilities to all diet items. We ran three simultaneous chains with 100,000 posterior draws each. We discarded the first 50,000 posterior draws for burnin and thinned to every 50th draw, resulting in 1000 posterior draws per chain and 3000 total draws from the joint posterior distribution. We assessed model convergence using the Gelman–Rubin and Geweke diagnostics. We used 95% Bayesian credible intervals to present measures of parameter estimate precision.

After obtaining proportion diet estimates for each raven chick, we used maximum likelihood methods to analyse spatio-temporal variance decomposition of raven feather isotopes comparing five randomintercept models for each isotope: year and nest, year only, nest only, hierarchical (nest 'nested' within year) and a null model (fixed intercept only) using Akaike's Information Criteria (AIC; Burnham & Anderson, 2002) and re-ran the final model using restricted maximum likelihood to obtain unbiased estimates of the variance components (Harville, 1977). Variance decomposition analyses were conducted in package 'Ime4' (Bates et al., 2015) in Program R (v. 3.2.2; R Core Team, 2015).

2.5 | Statistical analysis of spatial patterns

After the spatially naïve Bayesian stable isotope mixing model, we modelled the proportion of each diet item within each raven nest as a function of seven landscape characteristics: four two-dimensional surfaces and three distance-based variables. For two-dimensional surfaces, average percent big sagebrush cover (range: 1.5%–15.6%) was calculated as average values within 800 m of the raven nest using a sagebrush cover layer developed by Homer et al. (2012). Mean

vegetation greenness (Normalized Difference Vegetation Index [NDVI]; range: 0.2–0.3) within 800 m of the raven nest was calculated from 2009 NAIP imagery using the standard equation: (Near infrared - visible red) / (Near infrared + visible red). Mean index of relative sage-grouse nesting habitat probability (range: 0 [low probability] to 5 [high probability]) within 800 m of the raven nest was calculated from an output raster layer described in Dzialak et al. (2013), which was a nesting resource selection function composed of quadratic sagebrush, distance to nearest mesic area and distance to nearest residential or agricultural structures variables (see Dzialak et al., 2013 for method and validation details). Density of actively producing energy development infrastructure (range: 0.0-6.0 structures/km²) within 800 m of the raven nest was calculated from a Geographic Information System date-stamped point layer obtained from the Wyoming Oil and Gas Conservation Commission (WOGCC, 2020). For distance-based variables, we measured distance (km) to nearest highway or railroad (range: 0.0-46.3 km), distance to nearest dump or transfer station (range: 2.9–26.6 km) and distance to nearest sage-grouse lek (range: 0.4-9.0 km). We also included one temporal predictor variable (Julian date) to adjust for changes in diet proportions over the raven nesting season. Post hoc, we compared the distribution of distance to lek between raven nests on anthropogenic structures and 1000 random locations. We calculated correlation coefficients and variance inflation factors to assess collinearity in the landscape predictors.

We used beta regression ('betareg' in Program R [v. 3.2.2; R Core Team, 2015]) to model among-nest variation in the estimated proportion of each diet item to total raven chick assimilated diet as a function of the eight spatio-temporal predictor variables (Ferrari & Cribari-Neto, 2004). Results from the beta regressions are presented here as the percent change in proportional diet contribution as determined from backtransforming the log odds coefficients into odds ratios, calculated as $\% = -(1 - \exp(\text{coeff}))^*100$. Full non-backtransformed results are available in Table S2.

3 | RESULTS

3.1 | Nest substrate

We located 109 active raven nests within our census of the study area. Of these, 95 (87.2%) were on anthropogenic structures, including oil and gas infrastructure, abandoned buildings, windmills, power lines and so forth (Figure 1). Only 14 nests (12.8%) were on natural substrates, either rock cliffs or trees.

3.2 | Stable isotope signatures

We collected raven chick feathers from a total of 173 individual chicks from 92 nests (64 chicks from 35 nests in 2013, 109 chicks from 57 nests in 2014). Nine of the nests were sampled in both 2013 and 2014; thus, we sampled a total of 83 unique raven nests. Sampled nests were predominantly on anthropogenic structures, with 80 (96.4%) of the unique nests on anthropogenic structures (primarily oil and gas infras-



FIGURE 3 Frequency of distance from the nearest greater sage-grouse lek for random locations and raven nests on anthropogenic structures in southcentral Wyoming, USA, 2013–2014

tructure and abandoned buildings) and only three nests (3.6%) on natural substrates. A majority (78.7%) of raven nests on anthropogenic structures were located within 5 km of the nearest sage-grouse lek, approximately equal to distances expected at random (Figure 3). The three nests on natural substrates were 1.9, 5.9 and 5.9 km from the nearest lek.

The raw mean δ^{15} N (*SD*; *n*) values of diet items were 8.98‰ (0.37; 17) for human hair, 6.22‰ (1.45; 6) for mammal fur, 6.93‰ (1.59; 13) for sage-grouse egg membrane, 7.26‰ (0.68; 6) for sage-grouse feathers and 11.09‰ (1.23; 179) for raven chick feathers. The raw mean δ^{13} C (*SD*; *n*) values for human hair were -17.27% (0.74; 17), -23.63% (0.81; 6) for mammal fur, -24.92% (1.01; 13) for sage-grouse egg membrane, -22.60% (1.06; 6) for sage-grouse feathers and -21.97% (1.11; 179) for raven chick feathers. After adjusting the isotope values from the sampled tissues to the likely tissue consumed by raven chicks, the full consumer-source isotope mixing space ranged from a mean δ^{15} N value of 1.54‰ to 11.09‰, and a mean δ^{13} C value of -28.33% to -19.12% (Figure 4).

Model selection results for variance structures strongly supported a hierarchical model structure with Nest subset within Year for both the δ^{15} N (Δ AIC = 20.61) and the δ^{13} C (Δ AIC = 42.63) values. Raven chicks among nests showed high overlap in the δ^{15} N values and a clearer shift from 2013 to 2014 in the δ^{13} C values (Figure S1). Variance decomposition analysis found that inter-nest (i.e. spatial) variation explained 66.8% of the variability in the δ^{15} N values and 33.6% of the variability in the δ^{13} C values (62.4%) and a smaller amount of the variation in the δ^{15} N values (29.8%). For both the δ^{15} N and δ^{13} C values, the amount of remaining variation explained by variability among individual chicks within the same nest was small (3.5% and 4.0%, respectively; Figure 5).

3.3 | Non-spatial diet composition

In both years of the study, mammal carrion was, on average, the predominant (49.8% and 66.5% in 2013 and 2014, respectively)



FIGURE 4 Tissue-adjusted δ^{13} C and δ^{15} N values for raven chicks and potential diet sources. Diet sources were adjusted to convert sampled tissue isotope ratios to the actual tissue of consumption (e.g. mammal carrion fur \rightarrow mammal carrion muscle); adjustment values were gathered from peer-reviewed scientific literature. Raven chick feathers were not adjusted in this graph to account for trophic discrimination, although trophic discrimination was incorporated in the diet mixing model. Error bars are ± 1 SD



FIGURE 5 Variance decomposition of the δ^{13} C and δ^{15} N values for common raven chick feathers in southcentral Wyoming, USA, 2013–2014

assimilated diet item for raven chicks (Figure 6a; Table S2). Anthropogenic food (8.8%, 34.5%), sage-grouse chick (7.5%, 11.3%) and sagegrouse egg (3.5%, 10.2%) comprised moderate levels of raven chick diet. Plants (0.5%, 6.0%) and insects (0.4%, 1.0%) comprised a small portion of energy assimilation. The carrion and anthropogenic food change appeared to drive the temporal shift to higher δ^{15} N values and lower δ^{13} C values in 2014 compared to 2013 (Figure S1). Underlying mean population estimates of diet composition, there was a high degree of inter-chick variability for several diet items indicating a high degree of diet specialization for many raven breeding pairs (Figure 6b). The median posterior estimate for the proportion of diet that was mammal carrion for individual chick ranged from 0.22 to 0.96, for anthropogenic food it was 0.01 to 0.57, for sage-grouse chicks it was 0.01 to 0.41, for sage-grouse eggs it was 0.01 to 0.31, for plants it was 0.00 to 0.29 and for insects it was 0.00 to 0.01. This meant, for example, that some raven chicks had up to 96% of their assimilated diet derived from mammal carrion or up to 31% of their diet derived from sage-grouse eggs. See Table S3 for average diet estimates for individual nests.

3.4 Spatially explicit diet composition

Spatial predictor variables ranged from being uncorrelated (sagebrush and well density, r = 0.005) to moderately correlated (sagebrush and sage-grouse nest probability, r = 0.627; Table S4). All variance inflation factors were less than 2.78, indicating little collinearity in the regression models.

Raven nests in landscapes with surrounding higher average habitat probability for sage-grouse nesting shifted their diets compared to lower average probability. For every 1-unit increase in the sage-grouse nesting probability index, the proportion of diet that was mammal carrion decreased by a rate of 20.5% (-34.2% to -3.9%). In contrast, the proportion of insects increased by a rate of 17.0% (0.5%-36.2%) and the proportion of plants increased by a rate of 31.5% (0.9%-71.5%) for each 1-unit increase in the index (Figure 7; Tables 1 and S5).

Proximity to sage-grouse leks was also related to several diet items. For each 1-km increase between the raven nest and the nearest lek, the proportion of diet from sage-grouse chick declined by a rate of 11.6% (-18.0% to -4.7%), sage-grouse egg declined by a rate of 9.0% (-15.9% to -1.5%) and insect sources declined by a rate of 5.5% (-10.8% to 0.1%; Figure 8; Tables 1 and S5). Oppositely, mammal carrion sources increased by a rate of 14.0% (6.5%-22.1%) for every 1 km further from a lek.

Carrion contributions were also lower in landscapes with greater vegetative productivity (i.e. higher average NDVI values). Distance to the nearest dump or transfer station was only related to sage-grouse egg diet sources, with egg contribution to raven diet increasing by 3.3% (-0.2% to 7.0%) for each 1-km increase in distance between the raven nest and the nearest garbage dump (Table 1).

Temporal trends in raven chick diet were also present for some diet items. From the earliest raven chick feather sampling date (15 May) to the latest (11 July), there was an average daily decrease in the contribution of sage-grouse eggs by 1.5% (-2.5% to -0.5%), a daily decrease in the contribution of plants by 2.0% (95% CI: -3.3% to -0.8%) and a daily decrease in the contribution of insects by 1.2% (95% CI: -2.0% to -0.5%). Anthropogenic food increased during the breeding season by 1.0% per day (-0.2% to 2.3%). There was no decrease in the proportion of sage-grouse chicks concomitant with the decrease in eggs (0.02% per day, 95\% CI: -0.90% to 0.95%).



FIGURE 6 Contributions of source diet items to assimilated common raven chick diets (a) and the mean posterior estimated proportion of each diet item across all chicks (b) for each sampled raven chick (circles) and density plots across all raven chicks, 2013–2014, southcentral Wyoming, USA. Circles (2013) and triangles (2014) were jittered vertically, but not horizontally, for display purposes

TABLE 1 Percent change in diet contribution of each individual diet item with a 1-unit increase in the spatial/temporal variable. For example, the proportion of raven diet composed of greater sage-grouse (GRSG) eggs declined by 9.0% for each 1 km further between the raven nest and the nearest sage-grouse lek. Estimates in bold were significant at $\alpha = 0.05$; those in non-bold were significant at $\alpha = 0.10$; those represented by a 'dash' were non-significant. See Table S3 for full results

		Diet item					
Variable type	Spatial/temporal variable	Sage-grouse chick	Sage-grouse egg	Mammal carrion	Insect	C ₃ Plant	Anthropogenic food
Spatial 2-D	Big sagebrush cover	-	-	-	-	-	-
	NDVI	-	-	-100.0%	-	-	-
	GRSG nesting habitat	-	-	-20.5%	17.0%	31.5%	-
	Energy development infrastructure	-	-	-	-	-	-
Spatial distance	Distance highway/RR	-	-	-	-	-	-
	Distance dump/transfer	-	3.4%	-	-	-	-
	Dist GRSG lek	-11.6%	-9.0%	14.0%	-5.5%	-	-
Temporal	Julian date	-	-1.5%	-	-1.2%	-2.1%	1.0%

Abbreviation: 2-D, Two-dimensional; NDVI; Normalized Difference Vegetation Index; RR, railroad.

4 | DISCUSSION

We used stable isotope analysis to reconstruct likely diets of common raven chicks. We then used landscape analyses to identify spatial patterns in assimilated diets. There was high spatiotemporal variability in the proportions of dietary items provisioned to chicks, and much of this variation was likely explained by the spatial configuration of landscape features and available food items near the nest. Most notably, adult ravens provisioned chicks with higher amounts of sage-grouse eggs, sage-grouse chicks, insects and less mammal carrion when the



FIGURE 7 Raven chick diet item contributions in relation to sage-grouse nesting habitat probability within 800 m of the raven nest in southcentral Wyoming, USA, 2013–2014. Shaded bands are 95% credible intervals

raven nest was located closer to a sage-grouse lek. Similarly, when in habitats with a high probability of nesting for sage-grouse, raven chicks ate less mammal carrion and more insects and plants, but did not eat more sage-grouse eggs or chicks. We hypothesize that this may be because high probability of nesting for sage-grouse reflects selection for general 'high-quality' habitat (i.e. higher plant and insect availability due to moderate sagebrush cover, proximity to mesic areas and greater distance from residential/agricultural structures; Dzialak et al., 2013), but high density of sage-grouse nests only occurs in high-quality habitat proximal to leks (Gibson, 1996, Holloran & Anderson, 2005). Anthropogenic food was not related to any spatial variables that we considered, only date, such that anthropogenic food carbon signatures increased over time.

Proximity to an active sage-grouse lek was an important indicator that determined the relative proportion of sage-grouse chick and egg content in raven chick diets. Further, a large proportion of raven nests occurred within \sim 1–5 km of a sage-grouse breeding lek. This has implications for potential depredation rates of sage-grouse nests by ravens. Holloran and Anderson (2005) found that \sim 86% of sage-grouse nests



FIGURE 8 Contribution of selected diet sources to assimilated common raven chick diets in relation to distance from the nearest greater sage-grouse breeding lek in southcentral Wyoming, USA, 2013–2014. Shaded bands are 95% credible intervals

were within 9.0 km of a lek, the farthest distance any of our raven nests were from a lek. We found that raven nests closer to sage-grouse leks had a significantly higher proportion of their diet made up of sagegrouse components, aligning with higher-than-expected densities of sage-grouse nests within 5 km of a lek (Holloran & Anderson, 2005) and our finding that a majority of raven nests were within 5 km of a lek. In many sagebrush steppe landscapes and sage-grouse habitats, natural elevated raven nesting substrates are rare (Coates et al., 2014; Howe et al., 2014). However, anthropogenic structures such as buildings, powerlines and energy development infrastructure are increasingly common, and have comprised from 78% (Howe et al., 2014) up to 96%-100% (Harju et al., 2018) of all nesting substrates (Figure 1). This often results in ravens using anthropogenic structures to nest in sage-grouse habitat, as we found in this study (87.2% in this study; Brockman et al., 2019; Gibson et al., 2018; Steenhof et al., 1993). Breeding raven pairs are then anchored within sage-grouse habitat (when they otherwise would not be), as breeding pairs tend to forage within 0.8-2.0 km of the nest (Harju et al., 2018; Rösner & Selva, 2005). Even if anthropogenic structures occur at random with respect to lek locations, this fidelity likely facilitates increased depredation of sagegrouse nests and chicks when the anthropogenic structures are close to leks. Removal of structures, destruction of raven nests or installation of raven nesting deterrents on anthropogenic structures within 5 km of a lek may have a disproportionately beneficial impact on populationlevel sage-grouse nest success.

The dominant energy source for raven chicks on average was mammal carrion. Coates et al. (2016) found an affiliation of raven occurrence and domestic livestock on rangeland, and livestock carrion would provide an energy-rich food source. After mammal carrion and anthropogenic food, we found that sage-grouse eggs and chicks were most prominent. Similarly, after analysing regurgitated pellets from breeding ravens, Stiehl and Trautwein (1991) found that avian tissues, particularly eggshells, feathers, bones and down, made up 38.4% of pellet items and Engel and Young (1989) found avian items in 30.7% of pellets. Although mammal carrion was the primary energy source, the proportional derivation of raven energy sources may be partially decoupled from their impacts on dietary item populations. For example, even if the assimilated energy from sage-grouse eggs and chicks is a minor energetic component of raven chick diets, the impact of ravens on sagegrouse populations could be substantial due to the importance of nest success and chick survival on sage-grouse population growth (Taylor et al., 2012).

Unexpectedly, anthropogenic food was unrelated to any of the spatial variables that we measured. Distance to the nearest dump or transfer station may have been unrelated to anthropogenic food proportions because the closest that a raven nest was to a dump or transfer station was 2.9 km and ravens will rarely travel that far from the nest (Harju et al., 2018; Rösner & Selva, 2005; Roth et al., 2004). Nonetheless, there was some dietary source providing the high δ^{13} C values (e.g. C₄ pathway plants; Cerling & Harris, 1999). One explanation is that general non-highway human littering on the landscape contributed trash and litter, perhaps associated with some of the oil

and gas field. Alternatively, Engel and Young (1989) found maize (a C4 plant) in 50.9% of raven pellets. Although there was no tilled agriculture within our study area (C. Olson, pers. comm.), it is possible that ravens scavenged domestic livestock that had been raised on C₄ sillage (e.g. maize) prior to being released onto rangeland, and the associated C₄-based livestock carrion δ^{13} C values resulted in altered raven δ^{13} C values (Bahar et al., 2005).

It is possible, and even likely, that some of the sage-grouse components were from avian species other than sage-grouse. However, evidence for this is weak. Of 10 assessed sagebrush steppe passerines that can co-occur with sage-grouse, only the vesper sparrow (Pooecetes gramineus) showed a high degree of overlap in habitat with that of sage-grouse (Rowland et al., 2006). Separately, video monitoring of the fate of 144 sagebrush obligate passerine nests found zero incidences of raven depredation (Hethcoat & Chalfoun, 2015), suggesting that our findings primarily represent raven depredation of sagegrouse nests and chicks of which ravens are known to be major predators (Coates et al., 2008; Lockyer et al., 2013). Finally, in an extensive literature review of 78 federally listed avian species in the United States and Canada, Coates et al. (unpublished data) found documented raven impacts on only seven species, with the most impacted species being greater sage-grouse. They found that similarities in nesting biology, particularly ground nesting with little to no concealing vegetation, were similar among all affected species. None of the other avian species with documented raven impacts occur in or near our study area.

Stable isotope diet reconstruction studies require the assumption that isotopic signatures of all potential diet items are known or sampled (Nielsen et al., 2018). To satisfy this assumption here, we sought to create broad categories of diet items that we expected would cover the isotopic space of non-sampled diet items (e.g. that mammal carrion samples would cover the breadth of isotope values for herbivore mammal species not sampled; e.g. mice [*Peromyscus* spp.]). Our spatial analysis also served as a form of validation in that spatial variation in diet items was predictable in many cases, and aligned with expected ecological patterns.

Managers concerned with sage-grouse populations may want to remove structures or deter nesting on anthropogenic structures by ravens within 5 km of an active sage-grouse breeding lek to avoid anchoring breeding ravens to these areas. Such nesting subsidies may drive the observed negative impacts of ravens on sage-grouse populations in other studies, as evidenced by the spatial patterns in sagegrouse egg and chick consumption observed here. In general, we found that the spatial composition of anthropogenic nesting substrates matters, with potentially negative cascading effects on sensitive prey species.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

CO conceived the original idea and field methodology and carried out the field work. SH designed and conducted the analysis and led the writing of the manuscript. All authors contributed critically to manuscript organization, content and revision of drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10. 5061/dryad.47d7wm3dk (Harju et al., 2021).

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