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Influence of anthropogenic subsidies on movements of common ravens

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Abstract: Anthropogenic subsidies can benefit populations of generalist predators such as common ravens (ravens; *Corvus corax*), which in turn may depress populations of many types of species at lower-trophic levels, including desert tortoises (*Gopherus agassizii*) or greater sage-grouse (*Centrocercus urophasianus)*. Management of subsidized ravens often has targeted local breeding populations that are presumed to affect species of concern and ignored "urban" populations of ravens. However, little is known about how ravens move, especially in response to the presence of anthropogenic subsidies. Therefore, subsidized ravens from distant populations that are not managed may influence local prey. To better understand this issue, we deployed global positioning system – global system for mobile communications transmitters to track movements of 19 ravens from September to December 2020 relative to 2 land cover types that provide subsidies: developed areas and cultivated crops. On average, ravens moved 41.5 km (±30.5) per day, although daily movement distances ranged from 0.13–206.1 km. Raven movement among cover types during the non-breeding season varied widely, with 100% of individuals each using land cover types that provide subsidy and other types at least once in the season. On 100% of days ravens used areas that did not provide subsidy, on 86.7% of days they used developed areas, and on 20.5% of days they used cultivated crops. Although on some days a raven would stay exclusively in areas that did not provide subsidy, there were no days in which a single raven ever stayed exclusively in developed or cultivated crops. Ravens moved shorter distances on days when they used subsidies more frequently. Further, time spent in developed areas and cultivated crops increased when ravens roosted closer to them, although this effect was greater for developed areas than for cultivated crops. Individual ravens were not associated exclusively with either of the subsidy-providing landscapes we considered, but instead all birds used both subsidized and other landscapes. Our research suggests that management of ravens during the non-breeding season and possibly during the breeding season, intended to reduce risk of predation on desert tortoises, will be most effective if conducted on a broad scale because of distances the birds travel and the lack of separation between putative "urban" and "natural" populations of ravens.

Key words: animal movement, *Centrocercus urophasianus*, common raven, *Corvus corax*, crops, development, *Gopherus agassizii*, greater sage-grouse, Mojave Desert, Mojave Desert tortoise, synanthropy

Anthropogenic subsidies can influence wildlife populations, communities, and even trophic structure and pathways (Boarman et al. 2006, Kristan and Boarman 2007, Esque et al. 2010, Rodewald et al. 2011, Dinkins et al. 2016, Berry et al. 2020). Subsidies can be defined as having direct influences, occurring as increases in resources used by the species being subsidized (Boarman 2003, Boarman et al. 2006, Ruffino et al. 2013), or having indirect influences, resulting from environmental change, such as increased primary productivity in croplands that provides food to prey of a predator. In either case, a common consequence of subsidies is that they increase the density of predator populations by increasing ecoregion-specific carrying capacity, which in turn may act through exclusion or predation to depress populations at lower-trophic levels (Kristan and Boarman 2007, Bui et al. 2010, Esque et al. 2010, Egan et al. 2020).

This pattern of an anthropogenic subsidy influencing predator populations that then regulate an unsubsidized species often plays out with members of the family Corvidae. For example, blue jays (*Cyanocitta cristata*), Steller's jays (*Cyanocitta stelleri*), common ravens (ravens; *Corvus corax*), and American crows (*C. brachyrhynchos*) all benefit from anthropogenic subsidies and, via nest predation, influence populations of birds in the midwestern (Rodewald et al. 2011) and the western United States (Marzluff and Neatherlin 2006). Ravens are of particular concern in arid regions of the western United States where their numbers have increased (Duerr et al. 2015, Sauer et al. 2017). Today they are known to be important, sometimes even primary, sources of mortality or population regulation for the desert tortoise (tortoise; *Gopherus agassizii*; U.S. Fish and Wildlife Service [USFWS] 2011) and greater sage-grouse (sage-grouse; *Centrocercus urophasianus*; Coates et al. 2020).

Raven populations in the United States have increased in recent years for a diverse set of reasons (Boarman and Heinrich 2020), and these birds use anthropogenic subsidies throughout the year and throughout all life stages. Subsidies for ravens are usually in the form of increases in food availability (Coates et al. 2020) or in nesting substrates (Coates et al. 2014*a*, Restani and Lueck 2020). There is evidence that both breeding and non-breeding ravens use subsidies (Harju et al. 2018) and that raven densities are higher in areas with subsidies (Kristan and Boarman 2003, Duerr et al. 2015, O'Neil et al. 2018, Coates et al. 2020). Furthermore, these positive effects for ravens have negative effects on nest survival and nest success of sage-grouse (Dinkins et al. 2016, Coates et al. 2020) and on survival of neonate and juvenile desert tortoise (Berry et al. 2013, Daly et al. 2019).

Despite the significance of predation by ravens on sensitive species, a number of questions remain about how subsidies influence raven populations. With a few exceptions (e.g., Harju et al. 2018), most studies of raven movements have been observational in design, and there is little known about how ravens move across the landscape in relation to anthropogenic subsidies. This is important because management of ravens generally is targeted on the local populations that are presumed to influence a species of conservation concern (as is the case for lethal management or precluding new landfills within 8 km of boundaries of existing tortoise conservation areas), does not consider distance from tortoise habitat, and considers "urban" ravens as less of a threat to "natural" tortoise populations (USFWS 2008). However, management that does not consider the scale of raven movements may not alter the abundance of those birds that are negatively influencing prey populations (Holcomb et al. 2021).

Understanding the extent to which subsidized ravens move is therefore important to the design of management plans to mitigate their impact on sensitive and vulnerable prey species. To address this need, we deployed global positioning system (GPS) – global system for mobile communications (GSM) transmitters on ravens to track their movements during the non-breeding season in the Mojave Desert, USA. Our objectives were to: (1) record the distance ravens travel each day during the non-breeding season and the source of subsidies they used; (2) evaluate how those travel distances were influenced by use of 2 sources of subsidies (agricultural crops or developed areas); and (3) evaluate if daytime use of a specific source of subsidy was influenced by the distance a raven roosted from that subsidy (e.g., if a raven roosts in a developed area, does it tend to stay in that developed area or does it move from that area that day).

Study area

This study was completed within the western portion of the Mojave Desert of southern California (Figure 1). The area is managed in part under the Desert Renewable Energy Conservation Plan (Bureau of Land Management [BLM] 2016) and the recovery plan for the Mojave population of the desert tortoise (USFWS 2011). The study area has a dry, subtropical desert climate with hot summers and cool winters (Commission for Environmental Cooperation 1997, 2011). Native vegetation within the Mojave Desert is typified by creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*),

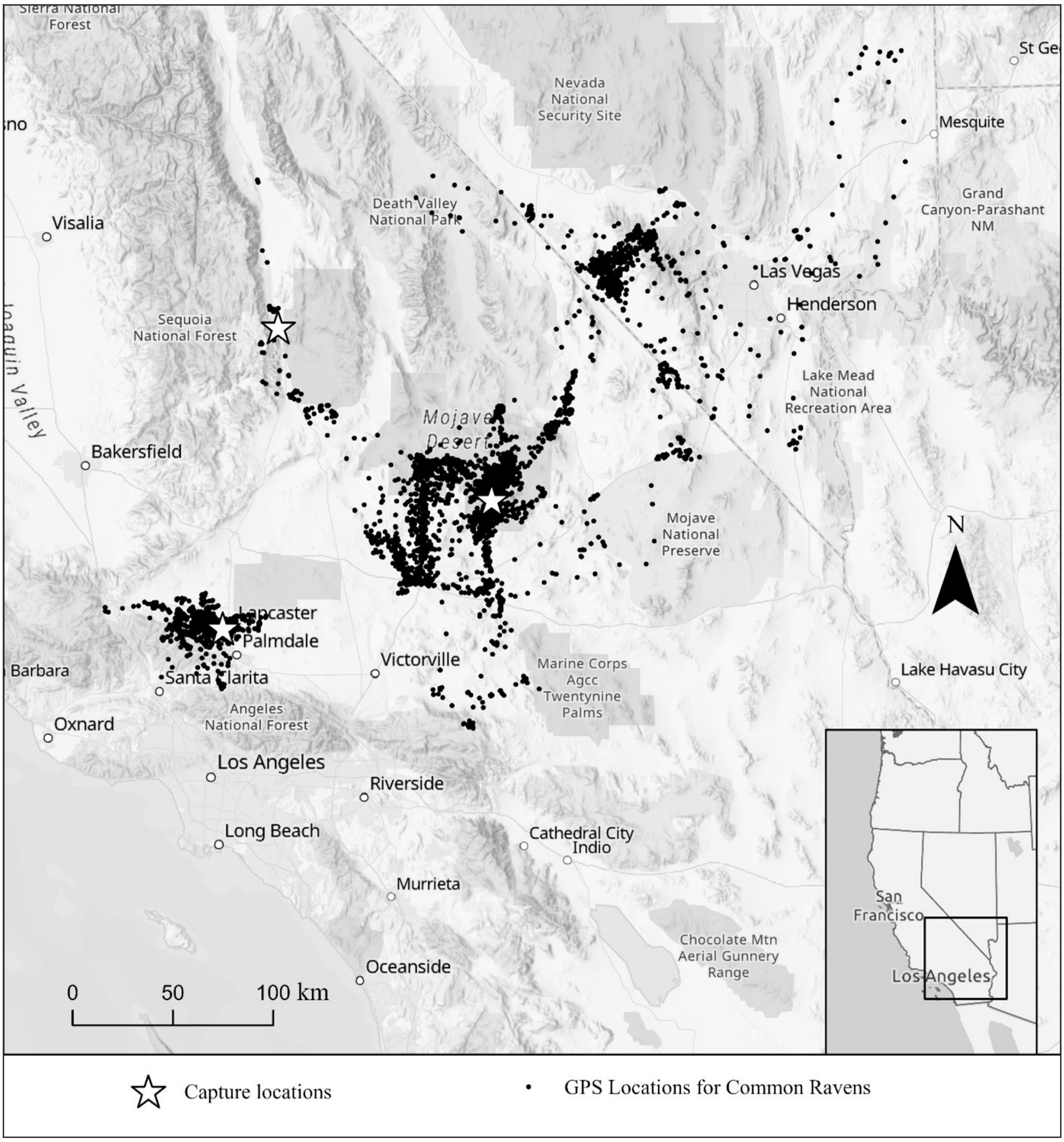

Figure 1. Global positioning system telemetry locations for 19 common ravens (*Corvus corax*) captured at 3 locations in the Mojave Desert, California, USA, September to December 2020.

and yuccas (e.g., Joshua tree, *Yucca brevifolia* or *Y. jaegeriana*). The Mojave Desert in California also supports several small- and medium-sized towns, including a few with human populations >100,000 that are connected by >60,000 km of roads.

Ravens are abundant throughout the Mojave Desert, both in native cover and human-dominated environments (Knight et al. 1999, Duerr et al. 2015). In less developed areas, ravens nest on cliffs and sometimes on trees, they forage in desert scrub habitats, and they are predators of invertebrate and vertebrate animals (Boarman and Heinrich 2020). In human-dominated environments, these birds will nest on power poles, road signs, buildings, and similar structures and will forage on crops, human refuse, and other anthropogenic food sources (Kristan and Boarman 2007). Ravens within the Mojave Desert are also a key predator of the desert tortoise and are thought to limit populations of this conservation-reliant species (Boarman 2003, Kristan and Boarman 2003, USFWS 2011, Daly et al. 2019, Berry et al. 2020, Holcomb et al. 2021). Furthermore, ravens cause conflict with infrastructure associated with transmission and distribution lines (Restani and Lueck 2020), and they cause damage to agricultural crops and livestock (Crabb et al. 1986, Marchand et al. 2018).

Methods

Capture and marking

We used bow nets and modified Swedish goshawk traps baited with carrion, rock doves (*Columba livia*), or anthropogenic food items (e.g., spaghetti and meatballs, turkey and stuffing) to capture ravens during the period from September 23 to December 2, 2020 (Meng 1971, Bloom 2015). Capture sites (indicated by stars in Figure 1) were near anthropogenic developments at Coso, Fort Irwin, and Lancaster, California, USA. We outfitted each raven we captured with an ES400W GPS-GSM transmitter (Cellular Tracking Technologies, Rio Grande, New Jersey, USA) attached with either backpack or leg loop harness mounts (Dunstan 1972, Rappole and Tipton 1991). In the case of ravens equipped with backpack mounts, we also clipped distal ends of the nape feathers to reduce feather interference with the solar panels of the transmitters.

Transmitters collected GPS locations at 15-minute intervals from sunrise to sunset and at 3 times during nighttime. Because sunrise and sunset vary with day length, the number of fixes collected per day varied. We filtered our telemetry data in 2 ways. First, we considered only GPS locations collected during the period that started the day after each bird was released and continued through December 6, 2020. Second, we included in our analysis only those 24-hour raven-days on which at least 20 GPS locations were recorded. Finally, we assumed that the first location of each 24-hour day, which was collected at nighttime, was the location at which the bird roosted.

Data processing

We used tracking analyst in ArcGIS (v. 10.6.1, ESRI, Redlands, California, USA) to measure the total distance (in km) that each raven moved over the course of a single day. We estimated that total distance by summing distances between sequential GPS locations each day. Subsequently, we determined the number of times per day that GPS locations fell within the 2 most prominent anthropogenically dominated land cover types in the study area (2016 National Land Cover Dataset [NLCD] classes 21–24, "developed" and 82 "cultivated crop"; Jin et al. 2019). To evaluate raven movements exclusively in the context of these 2 sources of subsidies, in our analyses we grouped other land cover types together.

Data analysis

Our analysis framework incorporated an information-theoretic approach (Burnham and Anderson 2002) to compare individual models within model sets. For each model set, we included all possible combinations of explanatory variables (Doherty et al. 2012), and we model averaged results when >1 model had support in the data (model weight > 0.0; Buckland et al. 1997, Burnham and Anderson 2002). Individual models were based on generalized linear mixed models (GLMMs) that included an intercept term and raven identification as a random effect to account for repeated measurements from individual ravens (Zuur et al. 2009). For analysis, we rescaled continuous variables by subtracting the mean of all observations and then dividing by the standard deviation of all observations. For each model set, we evaluated if pairs of explanatory variables had a correlation coefficient >0.7 (Dormann et al. 2018; none were correlated to this degree). Analyses were completed within Program R (R Development Core Team 2021).

We used GLMMs (package "nlme"; Pinheiro et al. 2021) to determine how travel distances of ravens were influenced by use of developed areas and cultivated crops. We considered presence of a raven within a cover type as use of that cover type. Our response variable in these models was daily distance traveled, which we square root transformed to improve normality of residuals (Supplemental Figure 1 compares different transformation approaches). Daily distance travelled was evaluated per raven and per day (i.e., the response variable consisted of a vector of observations, one for each raven-day). In all models, we specified an autoregressive correlation structure (AR1) to account for correlation of GPS data between successive days. We included 4 explanatory variables in these models. The first 2 variables were the number of locations per day within (1) developed areas and (2) cultivated crops. The second two were categorical variables that indicated whether the first daily location (roost) was within (3) developed areas or (4) cultivated crops. Our model is described by the following equation:

$$\sqrt{d_{ij}} = \beta_0 + (\beta_1 \times b_{ij}) + (\beta_2 \times c_{ij}) + (\beta_3 \times f_{ij}) + (\beta_4 \times g_{ij}) + e_{ij}$$

where *d* is the daily distance raven *j* traveled on day *i*, *b* is the number of locations within developed areas, *c* is the number of locations within crops, *f* and *g* are indicator variables that identify whether the first location was within developed or cultivated crops, respectively, and *e* is a random variable for raven individual and takes the form of an AR1 correlation structure.

We compared support in data for 16 models using the MuMIn package (Barton 2020). We also ran the full model with an additional fixed predictor for number of GPS locations per raven per day, to evaluate the relevance of including this term in our models.

We used zero-inflated GLMMs (package "GLMMadaptive"; Rizopoulos 2021) and negative-binomial distributions (Zurr et al. 2009) to determine whether daytime use of a specific type of subsidy was influenced by distance of the roost used that day to that subsidy. For this analysis, we created separate model sets for each subsidy source (developed and cultivated crops). The response variable was a count of the number of GPS locations per day that fell within that subsidy (indicative of time spent in the subsidy). Our sole explanatory variable was the distance from the overnight roost location to the nearest subsidy of that source (hereafter "roosting distance"), again, per raven and per day.

Zero-inflated models include 2 components. One is the zero-inflated component that uses logistic regression to model a binary response of 0 counts compared to all other counts. The zero-inflated component identifies extra 0s (inflated counts of 0) in the response variable. Output from this component is in the form of log-odds, which we convert to an estimate of the probability of a raven not using each subsidy source. The second component is conditional on removal of extra 0s (i.e., after accounting for the probability of not using a given subsidy). This conditional component is a linear regression that uses a negative-binomial distribution to model the relationship between the response and explanatory variables.

Zero-inflated models include explanatory variables for both the zero-inflated component and the conditional component. Our models were described by the following equation:

$$\mu_{ij} = e^{\beta_0 + (\beta_1 \times d_{ij}) + e_{ij}} \mid \pi_{ij} = \frac{e^{\gamma_0 + (\gamma_1 \times d_{ij}) + e_{ij}}}{1 + e^{\gamma_0 + (\gamma_1 \times d_{ij}) + e_{ij}}}$$

where μ is the mean count of locations within the subsidy source for raven *j* on day *i*, *d* is the distance between the roost location and the subsidy source (developed or cultivated crops), and *e* is a random variable for raven individual. Additionally, μ is conditional upon π, which is the probability for raven *j* on day *i* that the observation was an extra zero.

We used the same sets of variables for both components. Models were configured to include either an intercept term only or an intercept and our 1 predictor of roosting distance. This approach allowed the response variable to be constant or to vary by distance from roost to subsidy, respectively. Thus, each model set (1 set for developed areas and 1 set for cultivated crops) included a total of 4 models (see results for details of those models).

Results

Distances traveled and use of subsidies

We captured and tracked 19 ravens and recorded 30,457 GPS locations over 1,178 raven-days (Figure 1). Of these GPS locations, 21,952 occurred within areas without the 2 subsidies we considered, 7,749 occurred within devel-

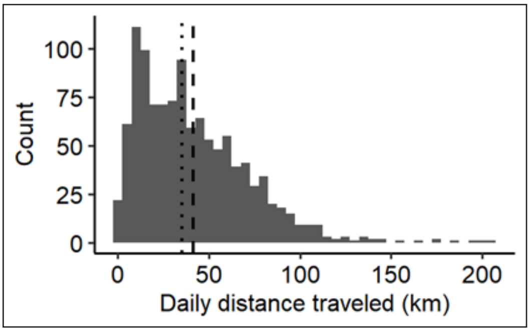

Figure 2. Daily distances travelled by common ravens (*Corvus corax*) in the Mojave Desert, California, USA, September to December 2020. Distances are shown as counts in bins of 5 km. Also shown are the mean (dashed line) and median (dotted line) of those daily distances.

Table 1. Linear coefficients (with standard error) for generalized linear mixed models evaluating effect of number of global positioning system (GPS) locations in, and roosting in, developed areas or cultivated crops on daily distance moved by common ravens (ravens; *Corvus corax*) in the Mojave Desert of California, USA, September to December 2020. Data were centered and scaled prior to analysis. All models included an autoregressive correlation structure (AR1) to account for spatial and temporal correlation between sequential GPS locations and a random effect for raven identification to account for repeated measurements from individual ravens. The full model (the second ranked in this table) included the 4 fixed effects below. AICc is Akaike Information Criterion, corrected for small sample size.

		Number of locations/day in		Roost in			
Model rank	Intercept	Developed	Crop	Developed	Crop	Δ AICc[a]	AICc weight[b]
1	5.64 (0.42)	-0.48 (0.08)	-0.61 (0.07)		-1.44 (0.39)	0	0.885
2	5.65 (0.42)	-0.48 (0.08)	-0.61 (0.07)	-0.02 (0.14)	-1.45 (0.39)	4.13	0.112
3	5.61 (0.42)	-0.48 (0.08)	-0.70 (0.07)			11.69	0.003
4	5.61 (0.43)	-0.48 (0.08)	-0.70 (0.07)	0.00 (0.14)		15.84	0.000
Averaged	5.64 (0.42)	-0.48 (0.08)	-0.61 (0.07)	-0.003 (0.05)	-1.44 (0.39)		

[a] AICc for the top model was 4591.8.

[b] Twelve models with AICc weight = 0.000 are not shown.

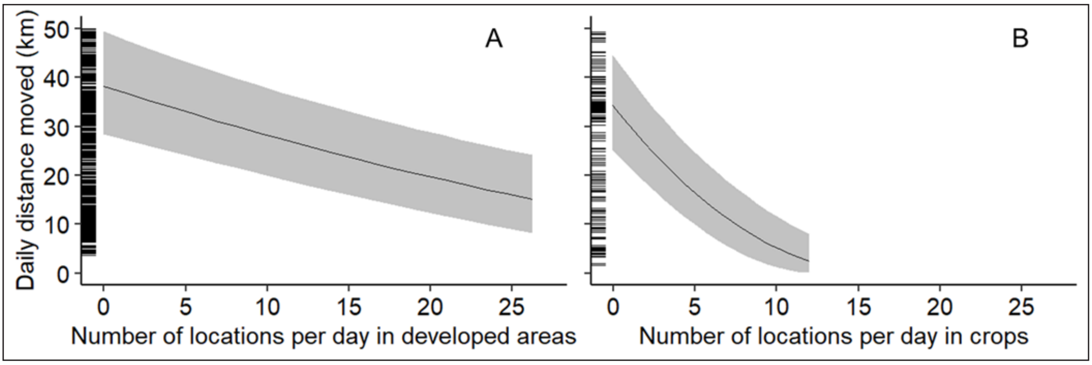

Figure 3. Response of daily distance moved to use of (A) developed areas and (B) cultivated crops for common ravens (*Corvus corax*) in the Mojave Desert of California, USA, September to December 2020. Daily distance moved (the y-axis) was truncated to 50 km for display, although it was not uncommon for birds to move farther within a day.

oped areas, and 756 occurred within cultivated crops (Supplemental Table 1). On average, GPS transmitters recorded 25.1 (±1.98, SD; [0,31], range) locations per day, of which 6.3 per day (±3.53, [0,26]) fell within developed areas and 0.5 per day (±0.9, [0,12]) within cultivated crops. We removed 50 raven-days from further consideration because GPS transmitters recorded <20 locations; the 1,128 remaining data points averaged 26.55 ± 1.49 locations per day, and there was no relationship between number of locations within a day and daily distance moved (Supplemental Figure 2).

Of the 1,128 raven-days used in analyses, on 8.6% of days the bird was exclusively within areas without the 2 subsidies we considered; in no cases was a bird exclusively within developed areas or within cultivated crops. Ravens used areas without subsidies on 100% of days monitored, developed areas on 86.7% of days, and cultivated crops on 20.5% of days. Ravens roosted in areas without subsidies (68.2% of days), developed areas (30.2%), and cultivated crops (1.6%). On average, ravens moved 41.5 km (±30.5) per day, although daily movement distances ranged from 0.13–206.1 km (Figure 2).

Influence of subsidy source on travel distance

The more that ravens used subsidies, the shorter distances they traveled. Three models

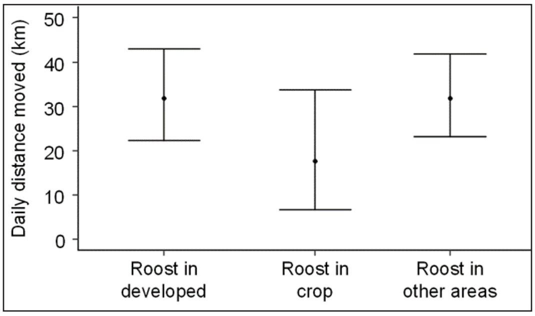

Figure 4. Differences in daily distance moved when starting the day at a roost in developed areas, cultivated crops, or other areas for common ravens (*Corvus corax*) in the Mojave Desert of California, USA, September to December 2020.

for the daily distance traveled by telemetered ravens had support in the data (Table 1). Model averaged effects suggest that daily distance traveled decreased as ravens used subsidies more often within a day, both for developed areas (Figure 3A) and cultivated crops (Figure 3B). Roosting within cultivated crops was also associated with shorter travel distances by ravens, but roosting within developed areas had no such effect (Figure 4). The full model with a fixed predictor for number of locations per raven per day performed substantially less well than did the full model without that term (Δ AICc = 4.1).

Influence of travel distance on use of subsidies

Ravens used subsidies more when they roosted within that subsidy. This was especially true when they roosted in developed areas and less so when they roosted in cultivated crops. Two models relating roosting distance to use of developed areas had support in the data (Table 2). For the zero-inflated component of the model, the first included a constant effect (intercept only), while the second included a distance effect. For the conditional component of the model, both models included distance effects. Model averaging of all components suggests there was a low probability (<0.10) that, on a given day, a given raven did not use developed areas (zero-inflated component; Figure 5A), and that when they did use developed areas, roosting closer to them was associated with using them for longer periods of time (conditional component; Figure 5B).

There was support in the data for 1 model that related roosting distance from cultivated crops to use of that subsidy (Table 3). This model included roosting distance as a predictor for both the zero-inflated and conditional components. There was a high probability (>0.80) that on a given day ravens did not use cultivated crops (zero-inflated component; Figure 5C), but when they did use cultivated crops, they were slightly more likely to have roosted closer to crops the night before (Figure 5D).

Plotting subsidy use as a function of roosting distances illustrates 2 important results. First, the distribution of distances between roosts and developed areas had a smaller range than that for distances between roosts and cultivated crops (rug plots, Figures 5A and 5B vs. Figures 5C and 5D), meaning that ravens never roosted >28 km from a developed area they used the following day, but they sometimes roosted as far as 80 km from a cultivated crop they used that following day. Second, roosting adjacent to developed areas increased the time spent in developed areas the following day (Figure 5B), whereas roosting adjacent to cultivated crops had little effect on time spent in cultivated crops (Figure 5D).

Discussion

Use of anthropogenic subsidies reduced movements of ravens, although the magnitude of effects differed by the source of subsidy. Furthermore, movement patterns varied widely among individuals, and, although some ravens moved short distances in a day, others moved very long distances, sometimes between widely dispersed human settlements. Despite this, it was rare for ravens not to use both areas with and without the subsidies we considered in a single day. All this has substantial implications for understanding these human–wildlife interactions.

On days that ravens spent longer periods of time in cultivated crops, they generally moved shorter distances than they did on days in which they spent similar or more time in developments (Figure 3). This suggests that resources available in cultivated crops (e.g., food, water; Coates et al. 2014*b*) may have a greater influence on raven movements than the resources provided within human developments. That said, ravens did not use crops frequently (about 1 location every 2 days), and 7 of 19 individuals tracked never used cultivated crops.

Table 2. Coefficients (with standard error) for conditional and zero-inflated components of generalized linear mixed models explaining number of global positioning system locations collected from common ravens (ravens; *Corvus corax*) that occur within developed areas as a function of the distance the birds roosted from developed areas in the Mojave Desert of California, USA, September to December 2020. Data were centered and scaled prior to analysis. These zero-inflated models included random effects to account for repeated measurements from individual birds and a single fixed predictor. Comparisons below illustrate performance of model pairs (zero-inflated component + conditional component) for models that included the fixed effect and those that were "intercept-only." AIC is Akaike Information Criterion.

	Zero-inflated components		Conditional components			
Model rank	Intercept	Roost distance from developed	Intercept	Roost distance from developed	Δ AIC	AIC
1	-2.72 (0.45)		1.85 (0.11)	-0.17 (0.02)	0.00	0.65
2	-2.7 (0.44)	0.11 (0.12)	1.85 (0.11)	-0.16 (0.02)	1.3	0.35
3	-2.77 (0.45)	0.22 (0.10)	1.88 (0.11)		55.6	0.00
4	-2.82 (0.46)		1.89 (0.11)		57.6	0.00
Averaged	-2.71 (0.44)	0.04 (0.07)	1.85 (0.11)	-0.17 (0.02)		

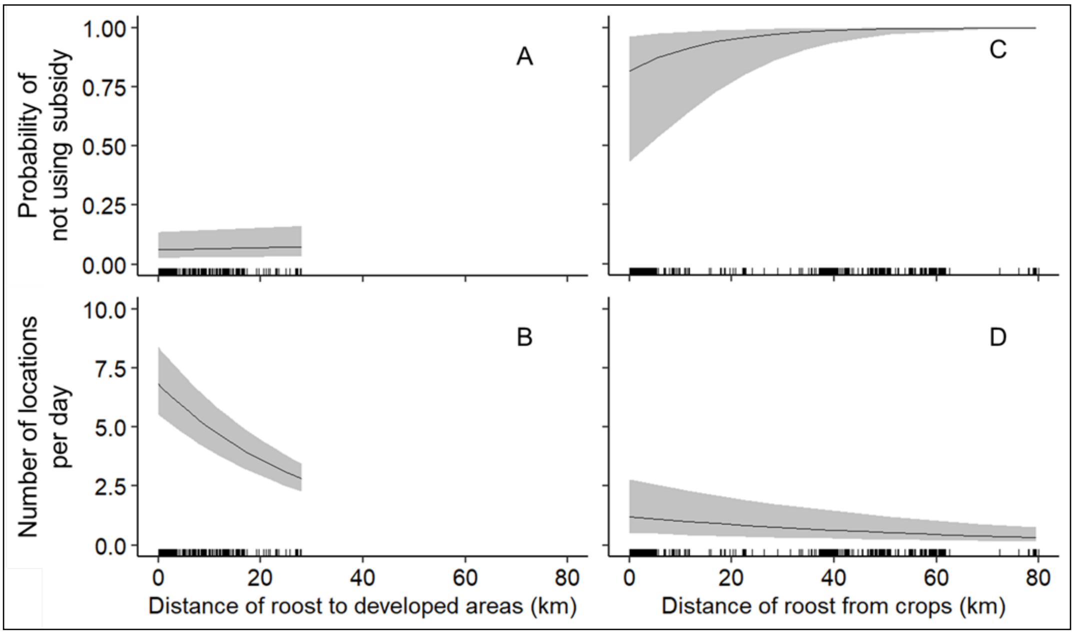

Figure 5. Responses of probability of not using a subsidy daily and number of locations per day to distance from roost to anthropogenic subsidies for common ravens (*Corvus corax*) in the Mojave Desert of California, USA, September to December 2020. One model used distance of roost to developed areas and included zero-inflated (A) and conditional components (B). A second model used distance of roost to cultivated crops, again including zero-inflated (C) and conditional components (D).

Therefore, although crops had a large influence on movements of some ravens, cultivated crops may provide a subsidy that is insufficient in quantity, availability, or attractiveness to influence all birds, and crops clearly are not used to the exclusion of other anthropogenic and natural resources.

In contrast to the irregular use of cultivated crops, all ravens used developed areas, and, on average, they roosted much closer to developed areas than to cultivated crops (Figure 5). One explanation for this use of developed areas may be because our trapping targeted birds near urban centers and we often used human food

Table 3. Coefficients (with standard error) for conditional and zero-inflated components of generalized linear mixed models explaining number of global positioning system locations collected from common ravens (ravens; *Corvus corax*) that occur within cultivated crops as a function of the distance the birds roosted from cultivated crops areas in the Mojave Desert of California, USA, September to December 2020. Data were centered and scaled prior to analysis. These zero-inflated models included random effects to account for repeated measurements from individual ravens and a single fixed predictor. Comparisons below illustrate performance of model pairs (zero-inflated component + conditional component) for models that included the fixed effect and those that were "intercept-only." AIC is Akaike Information Criterion.

	Zero-inflated components		Conditional components			
Model rank	Intercept	Roost distance from crops	Intercept	Roost distance from crops	Δ AIC	AIC weights
1	3.41 (0.91)	1.68 (0.23)	-0.23 (0.42)	-0.37 (0.07)	0.00	1.00
2	2.25 (1.21)		-0.79 (0.54)	-0.72 (0.08)	62.4	0.00
3	3.62 (0.89)	1.78 (0.22)	0.14 (0.41)		26.2	0.00
4	3.14 (0.95)		0.1 (0.5)		137.0	0.00

as bait. Alternatively, this could be because developed areas were both more abundant and more evenly distributed throughout the Mojave Desert than were cultivated crops, as evidenced in part by the greater roosting distances for crops than for developed areas (rug plots, Figures 5A and 5B vs. Figures 5C and 5D).

An atypical component of this analysis is that we focused on raven movements during the non-breeding season (e.g., see "summer" studies in Roth et al. 2004; Kristan and Boarman 2007; Coates et al. 2014*a*, 2020). Management of raven populations to enhance survival of threatened wildlife likely will be most effective if it takes into account movements during both the breeding and non-breeding periods of their life cycle. Much of the prior work on these birds has focused on breeding periods, presumably because this is both when most management of raven populations is applied (e.g., addling eggs through oiling; Shields et al. 2019) and when impacts to some wildlife species occur (nest predation to sage-grouse; Harju et al. 2018) or are most obvious (e.g., one can see the accumulation of tortoise carapaces below raven nests; Kristan and Boarman 2003, Daly et al. 2019). However, non-breeding periods account for a greater portion of the year than do breeding periods, and they include energetically costly activities such as molting and overwintering that can be influenced by subsidies and that can influence raven survival rates and carrying capacity. Furthermore, many of the species affected by raven predation are also available as prey outside the nesting season (although desert tortoise often overwinter underground; USFWS 2011). Because of this, these non-breeding periods likely account for a majority of the raven population's food consumption, meaning that effective management of ravens will depend in part on understanding their movements and behavior during this key period.

When interpreting the results of this work, there are several caveats to bear in mind. Although our sample size was large compared to similar telemetry studies in the Mojave (e.g., Braham et al. 2015), it is at the minimum for reliable inference in studies with questions with simple outcomes (Lindberg and Walker 2007). Likewise, by focusing on non-breeding season effects, we filled an important knowledge gap, but our inference is limited to 1 period of year. Future work also may wish to consider these patterns in a use-availability context (Johnson 1980) and for birds whose territorial status is known, to further understand nuance of how ravens use the landscape. Finally, the NLCD dataset we used is, from many perspectives, the best available, but it is also limited in at least 2 important regards. First, linear features such as powerlines and roadways provide important subsidy to ravens (Coates et al. 2014*a*), yet they are ineffectively captured with NLCD data. Although by focusing on 2 well-defined NLCD land cover classes we mitigate some of these issues, future analysis of the impact of subsidies on ravens may wish to more explicitly account for these important landscape features. Second, we observed that solar fields were often misclassified as NLCD category 81 (pasture/hay). Because of the way we structured our analysis (i.e., a comparison of use of 2 subsidized land cover types relative to use of all other land cover types), this is unlikely to impact inference we draw. That said, solar fields could provide some subsidy that we did not measure and, in some cases, could be important to ravens. As solar energy systems cover more land in the Mojave Desert, perhaps these landscapes will be described in other datasets that can be used for analyses such as ours (as they are for wind energy; see Hoen et al. 2018).

Management implications

Patterns of use by ravens of anthropogenic subsidies illustrate the likely complexity of options for management of raven predation on sensitive wildlife in the Mojave Desert. Even though the breeding season is when tortoise predation is most obvious and is the time period when raven reproduction is managed, raven behavior and demography outside of this time period will influence the effect of this species on sensitive and vulnerable prey. Our work demonstrated that during the non-breeding season, locations of individual ravens were not exclusively associated only with either anthropogenic or natural landscapes, but instead all birds used both types of landscapes (i.e., there was no such thing as an "urban" or a "natural" raven population). Thus, targeted removal of ravens, whether within critical habitat units, head-starting sites for tortoise, "raven concentration areas," or raven feeding areas, may affect local breeding birds but may not reduce predation rates by ravens traveling long distances from subsidies to removal areas. That may be particularly the case if a subsidy the ravens use is not simply food-based but also influenced by availability of roosting and nesting sites that occur along the long linear features not well captured by the NLCD dataset. Management of ravens during the non-breeding season, and possibly during the breeding season as well, intended to reduce risk of predation on tortoises will be most effective if conducted on a broad scale because of distances the birds travel and the lack of separation between putative "urban" and "natural" populations of ravens.

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Supplemental material

Supplemental material can be viewed at https://digitalcommons.usu.edu/hwi/vol15/iss3/9.

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