Spatial modeling of common raven density and occurrence helps guide landscape management within Great Basin sagebrush ecosystems

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Abstract: Common ravens (*Corvus corax*; ravens) are a behaviorally flexible nest predator of several avian species, including species of conservation concern. Movement patterns based on life history phases, particularly territoriality of breeding birds and transiency of nonbreeding birds, are thought to influence the frequency and efficacy of nest predation. As such, predicting where on the landscape territorial resident and non-territorial transient birds may be found in relation to the distribution of sensitive prey is of increasing importance to managers and conservationists. From 2007 to 2019, we conducted raven point count surveys between mid-March and mid-September across 43 different field sites representing typical sagebrush (*Artemisia* spp.) ecosystems of the Great Basin, USA. The surveys conducted during 2007–2016 were used in previously published maps of raven occurrence and density. Here, we examined the relationship between occurrence and density of ravens using spatially explicit predictions from 2 previously published studies and differentiate areas occupied by higher concentrations of resident ravens as opposed to transients. Surveys conducted during 2017–2019 were subsequently used to evaluate the predicted trends from our analytical approach. Specifically, we used residuals from a generalized linear regression to establish the relationship between occurrence and density, which ultimately resulted in a spatially explicit categorical map that identifies areas of resident versus transient ravens. We evaluated mapped categories using independently collected observed raven group sizes from the 2017–2019 survey data, as well as an independent dataset of global positioning system locations of resident and transient individuals monitored during 2019–2020. We observed moderate agreement between the mapped categories and independent datasets for both evaluation approaches. Our map provides broad inference about spatial variation in potential predation risk from ravens for species such as greater sage-grouse (*Centrocercus urophasianus*) and can be used as a valuable spatial layer for decision support tools aimed at guiding raven management decisions and, ultimately, improving survival and reproduction of sensitive prey within the Great Basin.

Key words: *Centrocercus* spp., common raven, *Corvus corax*, density, Great Basin, occurrence, predator–prey, sage-grouse, space use, species distribution models, transients

Common ravens (*Corvus corax*; ravens) are a behaviorally flexible predator species widely distributed throughout the northern hemisphere (Boarman and Heinrich 1999; Harju et al. 2018). In western North America, ravens' behavioral plasticity and opportunistic utilization of anthropogenic resources have led to dramat-ic population increases over the past several decades (Boarman and Heinrich 1999, Sauer et al. 2017). Raven use of human-related food resources (e.g., landfills, roadkill, cereal crops, artificial water resources) and habitat (e.g., transmission towers, roads, housing, powerlines) are well documented (Knight and Kawashima

1993, Webb 2004, Kristan et al. 2004, Howe et al. 2014, Coates et al. 2016*a*). In some areas, raven population increases have been tied directly to increases in human development (Austin 1971, Knight and Kawashima 1993, Kristan and Boarman 2003). As raven populations have grown, researchers and managers have increasingly documented negative relationships between raven occurrence or density and variation in nest and/or juvenile survival for several species, including species of conservation concern like snowy plovers (*Charadrius nivosus*; Burrell and Colwell 2012), desert tortoises (*Gopherus agassizii*; Boarman 2003), marbled murrelets (*Brachyramphus marmoratus*; Peery and Henry 2010), and greater sage-grouse (*Centrocercus urophasianus*; sage-grouse; Bui et al. 2010, Coates et al. 2010, Coates et al. 2020*a*).

Predation by ravens is a complex phenomenon thought to be influenced by a multitude of factors, including but not limited to raven population demographics such as breeding status, age, foraging patterns, and movement behavior (Kristan and Boarman 2003, Webb et al. 2011, Howe and Coates 2015). Such demographics also impact raven population structure and distribution, which in turn may impact the efficacy of management actions taken to mitigate raven predation (Bui et al. 2010). Traditionally, tools like species distribution models are used to map spatial heterogeneity in population distributions or demographics by mapping species occurrence or abundance in relation to environmental characteristics (Elith and Leathwick 2009, Merow et al. 2014). However, mapping species distribution in relation to demographic characteristics (e.g., breeding status, foraging patterns) remains challenging, especially for generalist species with broad ecological niches such as ravens (Guisan and Thuiller 2005, McPherson and Jetz 2007). Difficulties in mapping population structure are numerous, especially when population structure characteristics are behavioral in nature (e.g., movement strategy) or variable over time (e.g., breeding status). However, accurately mapping such demographics may not only improve understanding of raven populations and distribution but ultimately may improve the efficacy of management actions by focusing resources to demographic classes of interest like certain breeding statuses (Harju et al. 2018).

Transient ravens (hereafter, transients) tend to be nonbreeding juvenile or subadult individuals, are not territorial, and typically move nomadically across the landscape in varying group sizes (Loretto et al. 2017, Harju et al. 2018). Transient ravens forage opportunistically as they move but will often aggregate in large numbers at anthropogenic point sources such as roadkill, landfills, center-pivot irrigation, and other human-subsidized food resources (Heinrich 1988, Restani et al. 2001, Loretto et al. 2017). Often, transient ravens will rely heavily on point sources but may still opportunistically forage in surrounding habitat and prey on native species, a phenomenon known as "spillover" predation (Schneider 2001, Kristan and Boarman 2003). Conversely, resident ravens (hereafter, residents) exhibit territorial behavior, where typically a breeding pair of adults defend a home range year-round and rarely leave their territory (Marzluff and Neatherlin 2006, Harju et al. 2018), though nest failure may lead to movements more characteristic of transient nonbreeders (Harju et al. 2018). Resident breeders typically forage within their territory, developing long-term spatial memory of resource distribution and availability within their home range (Fagan et al. 2013, Beck et al. 2020). Because of their increased familiarity with food resources within their territories, resident breeders may be more likely to target native prey items than nonbreeders that forage more opportunistically over larger areas (Bui et al. 2010, Harju et al. 2018, Daly et al. 2019), and localized observations of nesting ravens' behaviors have lent support to this hypothesis (Howe and Coates 2015, Brussee and Coates 2018). By utilizing native prey as well as anthropogenic subsidies, when resident raven populations are large enough, their predation rates and impacts are decoupled from prey population dynamics (Courchamp et al. 2000, Kristan and Boarman 2003). Although raven populations likely have some influence on prey demographic rates regardless of the raven population structure (e.g., age structure and proportion of breeding adults), their relative effects on prey species are likely to vary in relation to these factors.

Because raven impacts to prey species may differ across space depending on relative concentrations of transients or residents, understanding the distribution and abundance

of both resident breeders and transient non-breeders at a broad, landscape level can influence management efforts to mitigate impacts of raven predation on sensitive prey species. For example, if habitats become saturated by territorial, resident ravens, the potential predation rates on prey may be greater than in situations where nonbreeding ravens occur more frequently but do not settle into resident behavioral patterns. Importantly, both circumstances may result in relatively high raven densities, with the former possibly having a disproportionate negative effect on native prey species. Although such nuances in the predator–prey relationship involving ravens and other species have long been suspected, the difficulty in studying these dynamics has largely prevented management efforts from focusing on problem areas beyond evaluations of local raven density (Bui et al. 2010, Dinkins et al. 2016, O'Neil et al. 2018a, Coates et al. 2020a).

Traditional methods for assessing distribution of residents and transients, including capture-mark-recapture techniques or deploying global positioning system (GPS) or very high frequency transmitters to monitor individuals over time are labor-intensive, expensive, and in many cases impractical at broad spatial scales (White 1982, Royle 2004, Rich et al. 2014). Instead, managers typically use noninvasive techniques like point counts of unmarked individuals to assess occurrence (ψ) or density ($\hat{D}$), but these techniques are usually unable to differentiate between resident and transient individuals because they do not assess individual behavior (MacKenzie et al. 2002, Efford 2004, Efford and Dawson 2012, Keiter et al. 2017). However, when considered together, relationships between density and occurrence derived from survey data may still have informative value when considering generalized patterns from a landscape perspective. Because residents typically will use and defend home ranges while rarely leaving them, predicted densities in areas with resident ravens may remain relatively low despite high probability of occurrence (Lopez-Sepulcre and Kokko 2005, Bui et al. 2010). Conversely, areas with relatively low occurrence probability may imply areas where ravens are less likely to maintain presence over time (i.e., not residents), but if many transient individuals are detected, as is common among flocks of non-territorial ravens exhibiting social behavior, then estimated densities may be relatively high despite lower occurrence probabilities. Areas with relatively high occurrence and high density imply that both resident and transient ravens may be present over time and should result in the highest overall densities. By considering spatially explicit relationships between both parameters, managers may be able to gain insight into the likely population structure across a region of interest and use this information to guide management decisions and actions.

Estimations of occurrence and density are both useful metrics of population status, and their relationship has been well studied (Linden et al. 2017, Parsons et al. 2017, Steenweg et al. 2018, Rogan et al. 2019). Occurrence estimates are based on repeated measures of the presence or absence of unmarked individuals at a defined site over time, and sites with high estimated occurrence are typically sites where the species of interest was detected across multiple sampling occasions at the same site (MacKenzie et al. 2002, MacKenzie and Royle 2005, Webb et al. 2014). In contrast, density estimates are derived from counts of marked or unmarked individuals at a site, often with a form of correction for detection probability, and sites with high estimated density occur where large numbers of individuals were detected (Efford 2004, Efford et al. 2009, Keiter et al. 2017). Density estimates may also reflect the net effect of other population processes like survival, recruitment, and, for species such as ravens, behavioral patterns such as sociality or territoriality (Both and Visser 2003, Rich et al. 2016, Rogan et al. 2019). True estimates of density and occurrence account for less than perfect detection of individuals ($P < 1$) and often incorporate the influence of environmental factors such as habitat characteristics, climatic conditions, distance to human structures or subsidies, and other environmental conditions likely to impact the species of interest (MacKenzie et al. 2002, Efford and Dawson 2012, Webb et al. 2014). Additionally, both parameters are often modeled spatially across predefined regions of interest to draw conclusions about habitat quality or suitability and to make management decisions (Efford et al. 2009, Mateo-Tomás and Olea 2010, Ramsey et al. 2015, Evans and Rittenhouse 2018). Al-

Figure 1. The Great Basin study area in the western United States.

though modeling of density and occurrence usually occurs independently in practice, the 2 estimates are inherently correlated, as estimates of density should scale with increases in occurrence while also depending on scale of estimation (Gaston et al. 2000, Royle and Nichols 2003, Linden et al. 2017).

Here, we examined the relationship between occurrence and density of ravens using spatially explicit predictions from 2 previously published studies (O'Neil et al. 2018*a*, Coates et al. 2020*a*) within the Great Basin region of the United States. Specifically, we estimated the amount of discrepancy between the 2 predictions as a continuous surface, which informed variation in the distribution and relative proportion of resident and transient individuals occurring throughout the region of interest. For example, we used discrepancies between the 2 modeled responses (density vs. occurrence) to differentiate areas likely occupied by higher concentrations of resident as opposed to transient ravens. While broad-scale information about raven density and occurrence has been developed previously, we expand on these products by developing a single predic-

tive surface that categorically identifies areas that might support different raven life history stages and delineates potential problem areas for elevated predation rates on sage-grouse or other species likely to be influenced by increasing raven populations.

Study area

Our study area encompassed sagebrush (*Artemisia* spp.) ecosystems within the Great Basin region of the United States, including Idaho, Nevada, and portions of Oregon and California, USA (Figure 1). The Great Basin is largely a high elevation semi-arid desert ecosystem, with elevations ranging from 341–3,995 m. Annual precipitation throughout the region ranges from 79–1,291 mm, which mainly falls as winter snow and early spring rain (Pilliod et al. 2017). Land uses included rangeland (livestock grazing primarily from cattle [*Bos taurus*], horses [*Equus caballus*], and domestic sheep [*Ovis aries*]), cropland agriculture (irrigated or dry), and federal Conservation Reserve Program. Vegetation communities were dominated by Wyoming big sagebrush (*Artemisia tridentate wyomingensis*), black sagebrush (*A. nova*), and low sagebrush (*A. arbuscula*) at low elevations (<2,100 m) and mountain big sagebrush (*A. t. vaseyana*) common at high elevations (>2,100 m; Coates et al. 2020*a*). Although the study area is largely a remote landscape with low human population density, human modifications of the environment are pronounced in the form of fragmentation from roads, electric transmission lines, communication towers, and industrial developments (e.g., agriculture, mining, and energy).

Methods
Data collection

From 2007 to 2019, we conducted raven point count surveys across 43 different field sites representing typical sagebrush ecosystems of the Great Basin. Surveys conducted between 2007 and 2016 (Coates et al. 2020*a*) were used in the initial spatial estimation of raven occurrence and density, while surveys conducted from 2017 to 2019 were used to evaluate predicted trends with subsequent analyses. We conducted surveys between mid-March and mid-September across all field sites each year. At each survey location, observers documented

all unique observations of ravens (individual or group) during a 10-minute point count. Observers recorded bearing, distance to the observed raven or group of ravens, and number of ravens observed. Complete details regarding survey methodology can be found in Coates et al. (2020*a*) and Brussee et al. (2021).

Spatial predictions from models of raven density and occurrence

Model and prediction of occurrence. We used existing spatial surfaces depicting predictions of raven occurrence (O'Neil et al. 2018*a*). Briefly, these surfaces provided estimates of the probability of raven occurrence within 2.57 km² survey units, where multiple point count surveys were conducted each year, while accounting for detection using a hierarchical occupancy modeling framework (MacKenzie 2006, Royle and Dorazio 2008). Occurrence (ψ) was the probability that the survey unit was occupied during the study season, given repeated surveys within and conditional on the estimated detection probability (P; probability observers recorded 1 or more ravens during a survey given that they were present). Using a hierarchical Bayesian modeling framework within the JAGS coding environment (Plummer 2003), predictor variables for viewshed, forested area, and livestock presence were included as covariates on detection probability, while predictors representing climate, vegetation, topography, and anthropogenic features were included as covariates to predict occurrence (O'Neil et al. 2018*a*).

From the parameter estimates of the most influential (i.e., selected) spatial predictors, O'Neil et al. (2018*a*) generated Bayesian posterior predictions of raven occurrence at each cell. The midpoint (i.e., value at highest probability) of the predictive posterior distribution represented the spatially explicit map of "true" raven occurrence (i.e., corrected for imperfect detection) for each map cell projected from covariates across the Great Basin. We used the resulting raster layer of occurrence in our examination of occurrence and density of ravens throughout the Great Basin. See O'Neil et al. (2018*a*) for further details on methods for modeling and mapping of raven occurrence.

Model and prediction of density. To represent density of ravens across the same area, we used previously developed spatial surfaces (Coates et al. 2020*a*). Briefly, Coates et al. (2020*a*) estimated annual raven densities across 43 study sites by implementing hierarchical distance sampling models from raven point count data (Royle et al. 2004, Sillett et al. 2012) in R package "unmarked" (Fiske and Chandler 2011). Distances at which ravens were observed during point counts were binned into 5 classes with breakpoints at 225, 450, 675, 900, and 1,125 m (e.g., Sillett et al. 2012, Kéry and Royle 2015). The relationship between raven distances and detection probability was estimated using a half-normal key function with covariates for area of viewshed and percent forested land cover within 1.125 km of the observer. Coates et al. (2020*a*) modeled density, conditional on the half-normal distance detection function, using a negative binomial abundance distribution with field site and year effects on abundance (Royle et al. 2004, Sillett et al. 2012) to represent site- and year-specific estimates of raven density.

The resulting estimates of raven density at each site-year combination were fit as a response variable in a random forest regression analysis (Breiman 2001) to explore relationships between these densities and environmental predictors representing climate, vegetation, topography, and anthropogenic features. Coates et al. (2020*a*) then developed spatial predictions of raven density across the Great Basin based on the selected environmental covariates that were included in the highest performing random forest model (Breiman 2001, Cutler et al. 2007, Murphy et al. 2010), and the resulting spatial surface was exported at a 1.30 km² spatial resolution and archived for public use (Coates et al. 2020*b*). We used this raster surface of spatially explicit raven density estimates to examine trends in occurrence and density of ravens throughout the Great Basin. See Coates et al. (2020*a*) for further details on methods for mapping raven density.

Analysis and map development. Prior to examining the relationship between occurrence and density, we resampled the occurrence raster surface to align with the resolution of the existing density surface (1.30 km²) using the nearest neighbor method in the "raster" package in Program R (Hijam 2020, R Development Core Team 2020). We examined the relationship between occurrence and density across the Great Basin using a generalized linear model (GLM)
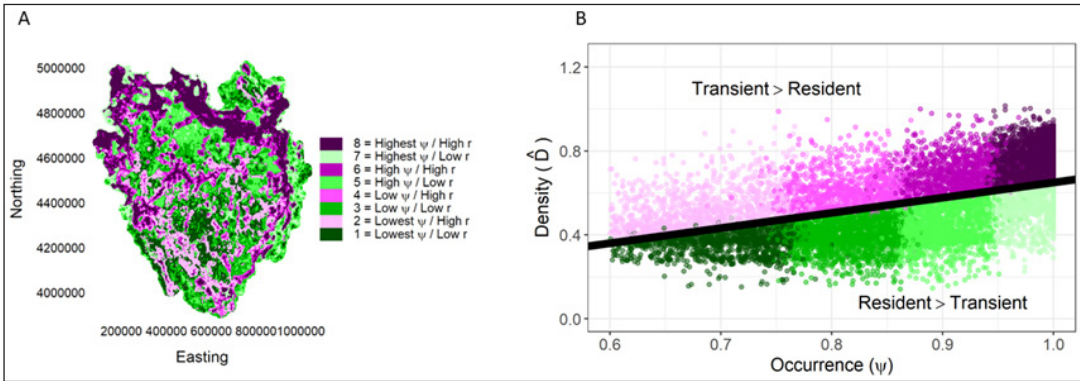
Figure 2. Thematic map (A) and scatter plot (B) of trends in common raven (*Corvus corax*) occurrence and density throughout the Great Basin study region, USA, based on data collected from 2007 to 2016. The black line in the scatter plot (B) represents the trend line from the generalized linear regression of occurrence and density.

that assumed a Poisson error distribution. We specified occurrence as the predictor variable and estimated density as the response variable, thus examining density as a function of occurrence. The sampling unit was each raster cell (1.30 km^2) on both surfaces. Because estimates of occurrence and density are inherently correlated (Gaston et al. 2000, Royle and Nichols 2003) and our existing estimates were unsurprisingly spatially correlated, our model did not meet the assumption of independence of variables (Beale et al. 2010, Montgomery et al. 2012). When this assumption is not met, the chance for type I error increases and model parameter estimates can become biased (Beale et al. 2010). However, we did not attempt to make any predictions of density based on model outputs. Instead, we focused our subsequent analysis on descriptive trends of the residuals from this GLM to draw conclusions about the variation in density and occurrence throughout the Great Basin. Model residuals represent the difference between observed and model-predicted estimates of the response variable (Montgomery et al. 2012) and thus provided information on the discrepancies between the model's expectation of density in relation to raven occurrence. The farther a residual value is from zero, the greater the difference between the estimated density and the expected density predicted from the occurrence surface, where positive values denote that estimated density was higher than expected based on the occurrence probability, indicating transient groups may be aggregating in these areas (Figure 2B). Conversely, negative values denote that estimated density was lower than expected

given the occurrence estimate and indicate that either the area has specific resources to support low numbers of residents and not larger groups of transient ravens, or territorial resident ravens are present and keeping densities lower than expected by defending areas from transient ravens (Figure 2B). We extracted the model residuals and visually examined them for normality and homoscedasticity. Residuals were spatially registered and thus could be projected as a continuous raster surface across the study area with a spatial resolution (i.e., pixel size) of 1.30 km^2.

To delineate trends in density and occurrence estimates, we categorized the residual surface into 8 distinct categories based on the distributional quantiles of both occurrence and residuals. To accomplish this, we first split the occurrence surface into quantiles where each category described the relative occurrence probability: "lowest ψ" = 0–25th percentiles, "low ψ" = 26–50th percentiles, "high ψ" = 51–75th percentiles, and "highest ψ" = 76–100th percentiles. We then intersected the occurrence quartiles with the residual surface and classified the intersections as either above or below the expected value (value falls on regression trend line) where "low r" = negative residual values and "high r" = positive residual values. The resulting "low" quantile can be interpreted as lower than expected densities for that occurrence quartile, while "high" quantile is interpreted as higher than expected densities for that occurrence quartile (Figure 2). The resulting thematic map had 8 categories that reflected relationships between occurrence and density estimates: category 1 = "lowest ψ/

low r," 2 = "lowest ψ/high r," 3 = "low ψ/low r," 4 = "low ψ/high r," 5 = "high ψ/low r," 6 = "high ψ/high r," 7 = "highest ψ/low r," 8 = "highest ψ/high r." We expected that disproportionately more resident ravens would be more likely in categories 5 and 7 while disproportionately more transient ravens would be more likely in categories 2 and 4. We expected that large numbers of both residents and transients would be found in categories 6 and 8, where both ψ and residuals were high (e.g., density and occurrence are both high). We created all mapping outputs using the ArcPy module for Python 3.6 (Python Software Foundation, http://www.python.org) and ArcMap 10.7 (Esri Inc., Redlands, California, USA).

After we evaluated the map for accuracy (see methods below), we present an example of how the map could be used to infer differences in predation risk for sage-grouse populations. We chose sage-grouse as an example because they are a sensitive prey species of high conservation concern in sagebrush ecosystems (Connelly et al. 2004). To do this, we intersected sage-grouse concentration areas with our map and quantified the area and percent area of each map category within the sage-grouse concentration areas. The sage-grouse concentration areas were based on predictive modeling of space use and abundance of breeding sage-grouse as well as models of sage-grouse resource selection during the same time period (approximately 2007–2016) our raven population data were collected (Coates et al. 2016b, Doherty et al. 2016). This analysis, although descriptive in nature, demonstrated how our map could be used to identify areas associated with potentially increased predation risk of sage-grouse by ravens.

Map evaluation

We used 2 different evaluation approaches to evaluate the ability of our mapped categories to describe variation in raven group sizes and individual raven spatial movements using independent datasets. For the first approach, we used point count survey data collected from 2017 to 2019 (independently of the point count survey data used to estimate occurrence or density) to assess the frequency of different raven group sizes in each category of the occurrence/residual surface. For each point count survey, observed group size was binned into 1

of 3 categories: null groups (0 ravens observed), small groups (1–2 ravens observed), and large groups (3+ ravens observed). By differentiating between small and large group sizes, we were able to establish a general threshold of group sizes that likely comprised transient ravens (i.e., large group of 3+ ravens; Loretto et al. 2017) as opposed to small group sizes that more likely comprised either resident or transient birds (Bui et al. 2010). We then overlayed the point locations of surveys with the occurrence/residual surface to assign each group size to a category of occurrence/residual trends and calculated the proportions of different group sizes within each map category.

We compared these proportions across various map categories of interest using a 2-tailed, 2 proportions z-test with continuity correction (Newcombe 1998). Specifically, we compared the combined proportions of null groups from categories 1 and 2 to the proportion of null groups in all other categories. This comparison allowed us to determine if the map categories with the lowest predicted occurrence had significantly fewer raven observations than map categories with higher predicted occurrence, thus accurately delineating trends in raven occurrence. We also compared the combined proportions of large groups from categories 6 and 8 against the combined proportions across all other categories to determine whether our map categories were accurately delineating areas where raven occurrence and estimated density were relatively high. Additionally, we compared proportions of large group sizes in category 4 (low occurrence/high residuals) to combined proportions of large group sizes in categories 1 and 3 to determine if our map categorization accurately captured areas where we expected to observe transient birds that may exhibit aggregation behaviors (Loretto et al. 2017). We used an alpha of 0.05 to determine statistical significance of comparisons.

Our second validation approach assessed whether resident and transient ravens monitored with GPS transmitters used areas on our categorical map in ways that were consistent with the occurrence-density relationship. For this approach, we used movements of ravens monitored within the Great Basin as part of a larger raven ecology study during 2019 and 2020. Ravens were captured by hand or using

hand nets and were fitted with GeoTrak GT-22GS-GPS transmitters (GeoTrak, Inc., Apex, North Carolina, USA) before being released at their capture location. All animal capture and handling practices were approved under Nevada Department of Wildlife permit 06715 or U.S. Geological Survey permit 21142. Transmitters were programmed to collect 8 locations (±100 m) per day to document raven movements. We only examined movement data from March to May to match the time period that point count survey data were collected to estimate occurrence and density as well as the time period that overlaps with raven nesting season (mid-March through July; Kristan and Boarman 2003). If individuals were monitored across multiple years, each year was considered independently because individual ravens can shift between residency and transiency across years, or in the case of nesting, residents can use different nest locations in subsequent years (Roth et al. 2004).

To determine whether a monitored raven was exhibiting resident or transient behavior, we examined each individual's site fidelity (i.e., staying in the same area over time) and home range patterns by generating 95% minimum convex polygons (MCP). We then calculated the area of each MCP and quantified the distance of each relocation from the centroid of the MCP to assess site fidelity and approximate size of home range of each individual during the monitoring period. We used the R package "adehabitatHR" for all MCP analyses (Calenge 2006). Previous research has found that resident individuals exhibit high site fidelity and use smaller areas than transient, nonbreeding individuals (Roth et al. 2004, Harju et al. 2018). However, individuals have been observed moving relatively long distances from their roost or nest (Engel and Young 1992), and our monitoring period likely included several days of movement locations prior to residents entering the nesting season (mid-March), so we used a conservative threshold of site fidelity combined with detailed visual assessment and confirmation to minimize misclassification of residents as transients and vice versa. Thus, we designated individuals that did not move >65 km from the center of their MCP and had an MCP area of <450 km² as residents, while individuals with longer distance movements and extremely large (>7,000

km²) MCPs were designated as transient. Notably, MCP estimation methodologies are known to overestimate space use of individuals (Borger et al. 2006). Our goal, however, was not to define home ranges for each individual, but rather to efficiently differentiate between residential and transient movement patterns by relating general site fidelity and space use to a conservative biological threshold. Using MCP methods to estimate space use allowed us to confidently differentiate between resident and transient birds because transient birds that moved large distances would generate large MCP estimates (>7,000 km²) relative to resident birds (<450 km²) exhibiting high site fidelity.

We used a use/availability approach (Beyer et al. 2010) to determine whether resident and transient birds' use patterns were consistent with mapped categories across the Great Basin. We generated randomly distributed point locations across the Great Basin, representing "available" map categories, at a 5:1 ratio to "used" GPS relocations. We then used GLMM with a binomial distribution and a logit link function to evaluate if residents and transients used certain map categories more frequently than expected given availability of those categories. Because we expected movement patterns to differ between resident and transient individuals and across years, we modeled each group separately for each year. We modeled the binary response of use (GPS location) and available (random location) as a function of different categories from the occurrence/residual surface predictions described above. This specification allowed us to estimate the influence of each occurrence/residual category on disproportionate use to availability. All models included individual as a random effect to account for differences in sample size among individual birds (Gillies et al. 2006). If models revealed that resident or transient individuals used a map category significantly more or less (α = 0.05) than it was available, we interpreted that as selection for or against that category. All models used category 1 as an intercept, so that estimated selection trends were interpreted as relative to predicted selection for category 1, the category with lowest occurrence and lowest residuals (i.e., areas of low use). We interpreted trends in raven selection for or against map categories from GPS data as evidence of whether our map accurately
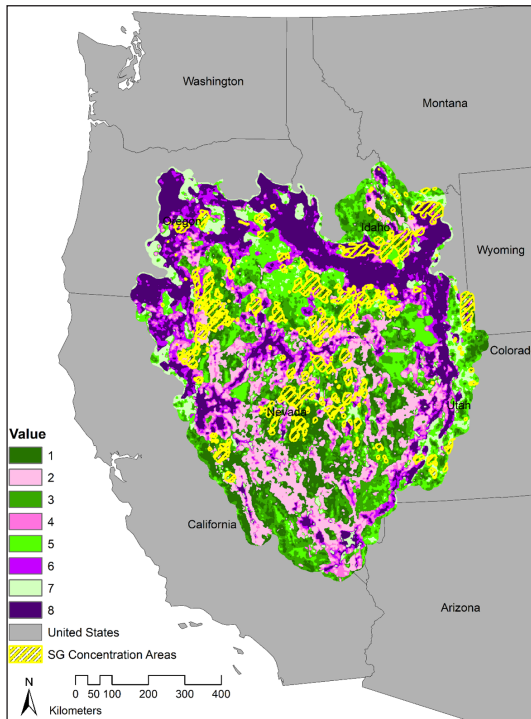
Figure 3. Greater sage-grouse (*Centrocercus urophasianus*) concentration areas overlayed on the thematic map of common raven (*Corvus corax*) occurrence and density across the Great Basin, USA, estimated from data collected between 2007 and 2016. Categories represented correspond to quantiles of occurrence and estimated residuals from a density model where category 1 = "lowest *ψ*/low *r*," category 2 = "lowest *ψ*/high *r*," category 3 = "low *ψ*/ low *r*," category 4 = "low *ψ*/high *r*," category 5 = "high *ψ*/low *r*," category 6 = "high *ψ*/high *r*," category 7 = "highest *ψ*/low *r*," category 8 = "highest *ψ*/high *r*."

Table 1. Quantified area of sage-grouse (*Centrocercus* spp.) concentration areas that fell in each category of a common raven (*Corvus corax*) occurrence and density map. Categories shown correspond to quantiles of occurrence and estimated residuals from a density model where category 1 = "lowest *ψ*/low *r*," category 2 = "lowest *ψ*/high *r*," category 3 = "low *ψ*/low *r*," category 4 = "low *ψ*/high *r*," category 5 = "high *ψ*/low *r*," category 6 = "high *ψ*/high *r*," category 7 = "highest *ψ*/low *r*," category 8 = "highest *ψ*/high *r*."

Map category	Area (km²)	Percent area (%)
1	8,339.10	14.66
2	4,847.28	8.62
3	9,970.44	17.52
4	7,097.64	12.47
5	11,412.54	20.06
6	7,379.22	12.97
7	5,655.54	9.94
8	2,197.92	3.86

predicted locations and space use of individual resident and transient ravens throughout the study area.

We then used a pairwise contrast analysis to test differences in relative selection of different map categories. We ran all pairwise comparisons between each map category but were specifically interested in comparisons across residual levels within each occurrence category (i.e., compare category 1 vs. 2, 3 vs. 4, etc.) to determine if our occurrence/residual map consistently differentiated between categories we might expect resident or transient birds to exhibit greater selection for (i.e., categories 1, 3, 5, 7 or 2, 4, 6, 8, respectively). We emphasized specific contrasts to evaluate support for hypotheses about resident versus transient use of the categorical map. For example, we expected greater resident selection for categories 5 and 7 relative to categories 1 and 2 to determine whether residents were disproportionately using areas with relatively high occurrence but low residuals. For transients, we expected greater selection for categories 2 and 4 (relatively low occurrence but high residuals) relative to categories 5 and 7 to determine if transients were selecting for areas with low occupancy/high residual relative to areas of high occupancy. This approach allowed us to assess how selection for all categories of our occurrence/residual map differed between resident and transient birds and whether selection patterns aligned with our predictions based on map categorization.

Results

We conducted 31,609 raven point count surveys from 2007 to 2019. Of those surveys, 16,974 were conducted between 2007 and 2016 and were used to model raven occurrence and density. We conducted 14,815 point count surveys from 2017 to 2019 that were used to evaluate how well our occurrence/residual map surface predicted where small (assumed resident) and large groups (assumed transient) of ravens would occur across the study area. Each of the 8 categories in the occurrence/residual map comprised approximately 12.5% (± 0.2%) of the Great Basin area (Figure 2). Upon overlaying the sage-grouse concentration areas with our map, we found that 46.8% of sage-grouse concentration areas fell in categories with high con-

Table 2. Counts and proportions of null (0), small (1–2), and large (3+) common raven (*Corvus corax*) group sizes observed in each thematic category of occurrence and residuals from a density model. Group sizes were obtained via 14,815 point count surveys conducted from 2017 to 2019 across the Great Basin, USA. Categories correspond to quantiles of occurrence and estimated residuals from a density model where category 1 = "lowest ψ/low r," category 2 = "lowest ψ/high r," category 3 = "low ψ/low r," category 4 = "low ψ/high r," category 5 = "high ψ/low r," category 6 = "high ψ/high r," category 7 = "highest ψ/low r," category 8 = "highest ψ/high r."

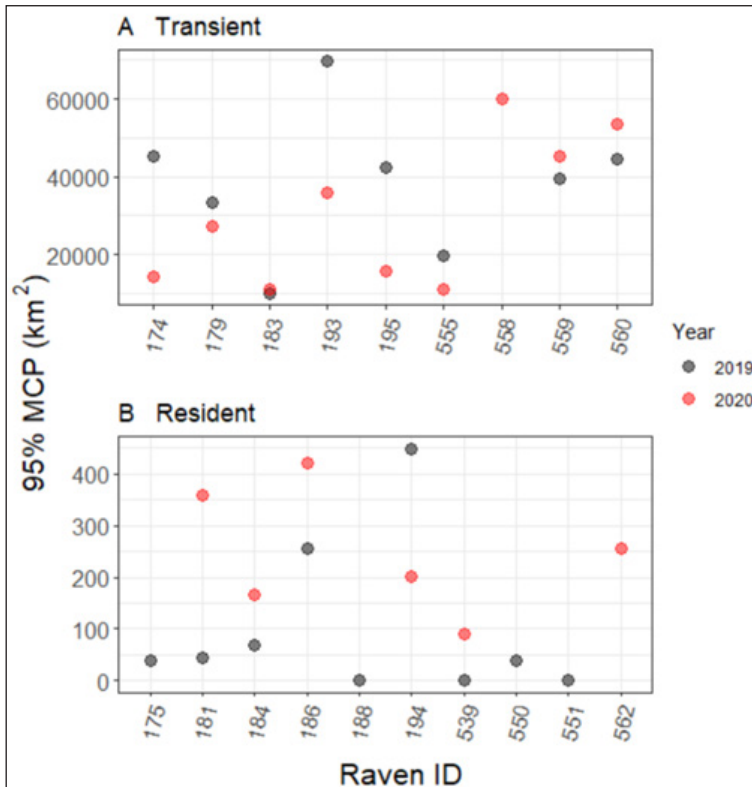| Category	Null group counts	Small group counts	Large group counts	Null group proportion	Small group proportion	Large group proportion
1	1,660	517	72	0.738	0.23	0.032
2	597	279	35	0.655	0.306	0.038
3	899	428	73	0.642	0.306	0.052
4	661	513	63	0.534	0.415	0.051
5	934	601	92	0.574	0.369	0.057
6	278	357	51	0.405	0.52	0.074
7	177	160	16	0.501	0.453	0.045
8	18	51	7	0.237	0.671	0.092

Figure 4. Ninety-five percent Minimum Convex Polygons (km²; MCP) of space use for resident (A) and transient (B) common ravens (*Corvus corax*) monitored in the Great Basin, USA, during 2019 and 2020. Birds monitored in 2019 are shown in gray, while birds monitored in 2020 are shown in red.

Table 3. Beta coefficient (β) estimates, standard error (SE), Z-values, and P-values (P) for generalized linear mixed models assessing resident and transient common raven (*Corvus corax*) use of each occurrence/residual map category in 2019 and 2020.

Status	Model covariate	2019				2020			
		β estimate	SE	Z-value	P-value	β estimate	SE	Z-value	P-value
Resident	Category 1 (intercept)	-6.12	0.56	-10.84	<0.001	-4.16	0.19	-21.66	<0.001
	Category 2	2.86	0.58	4.91	<0.001	1.31	0.21	6.11	<0.001
	Category 3	0.88	0.68	1.30	0.19	1.38	0.21	6.54	<0.001
	Category 4	5.28	0.57	9.33	<0.001	3.73	0.19	19.37	<0.001
	Category 5	1.78	0.61	2.92	0.004	0.96	0.22	4.31	<0.001
	Category 6	4.72	0.57	8.31	<0.001	3.45	0.19	17.84	<0.001
	Category 7	4.78	0.57	8.42	<0.001	2.19	0.20	10.93	<0.001
	Category 8	5.63	0.57	9.95	<0.001	2.41	0.20	12.16	<0.001
Transient	Category 1 (intercept)	-2.07	0.07	-28.38	<0.001	-2.62	0.08	-32.40	<0.001
	Category 2	0.63	0.09	6.80	<0.001	1.03	0.10	10.85	<0.001
	Category 3	-1.04	0.14	-7.51	<0.001	0.44	0.10	4.22	<0.001
	Category 4	0.66	0.09	7.19	<0.001	2.03	0.09	23.07	<0.001
	Category 5	-1.49	0.16	-9.116	<0.001	0.54	0.10	5.25	<0.001
	Category 6	1.04	0.09	11.96	<0.001	1.65	0.09	18.37	<0.001
	Category 7	0.69	0.09	7.61	<0.001	-0.002	0.12	-0.02	0.99
	Category 8	0.92	0.09	10.35	<0.001	0.08	0.11	0.70	0.48

centrations of resident ravens (categories 5, 6, 7, 8; Figure 3; Table 1). Of these areas, ~17% fell in categories 6 and 8, where we expected high concentrations of both residents and transients, while ~30% fell in categories 5 and 7, where we expect high concentrations of only residents. Spatially explicit data output maps are available online (Coates et al. 2021).

When evaluating group sizes (2017–2019), sampling effort varied across categories (Table 2). The most frequently observed group size across categories 1–7 was the null group size (0 ravens observed), while the small group size was the most frequently observed group size in category 8. Categories 1 and 2 had a higher proportion of null group sizes relative to all other categories, indicating that the map product was accurately describing areas with lowest occurrence. Conversely, categories 6 and 8 had a significantly higher proportion of large group sizes relative to other categories. We found no significant difference between the proportion of large group sizes in category 4 relative to categories 1 and 3.

We used GPS location datasets of 22 ravens, 10 of which were monitored for both years, resulting in 32 unique movement datasets for subsequent analysis. We classified 15 of the datasets as resident birds (*n* = 6 for 2019 and *n* = 9 for 2020) and 17 as transient (*n* = 7 for 2019 and *n* = 10 for 2020; Figure 4). Based on our classification, 5,155 resident locations and 6,244 transient locations were used in modeling analyses. Modeling revealed that resident ravens showed significantly stronger selection for all map categories except category 8 relative to categories 1 and 3 in 2019 (Table 3). Transients in 2019 selected for categories 2, 4, 6, 7, and 8 significantly more than category 1 and exhibited avoidance of categories 3 and 5 (Table 3). Resident and transient ravens in 2020 showed selection for all categories relative to category 1. These findings mostly aligned with our expectations of residents selecting categories 5–8 (i.e., areas with high probability of occurrence regardless of density), while categories 2, 4, 6, and 8 (i.e., areas with high density
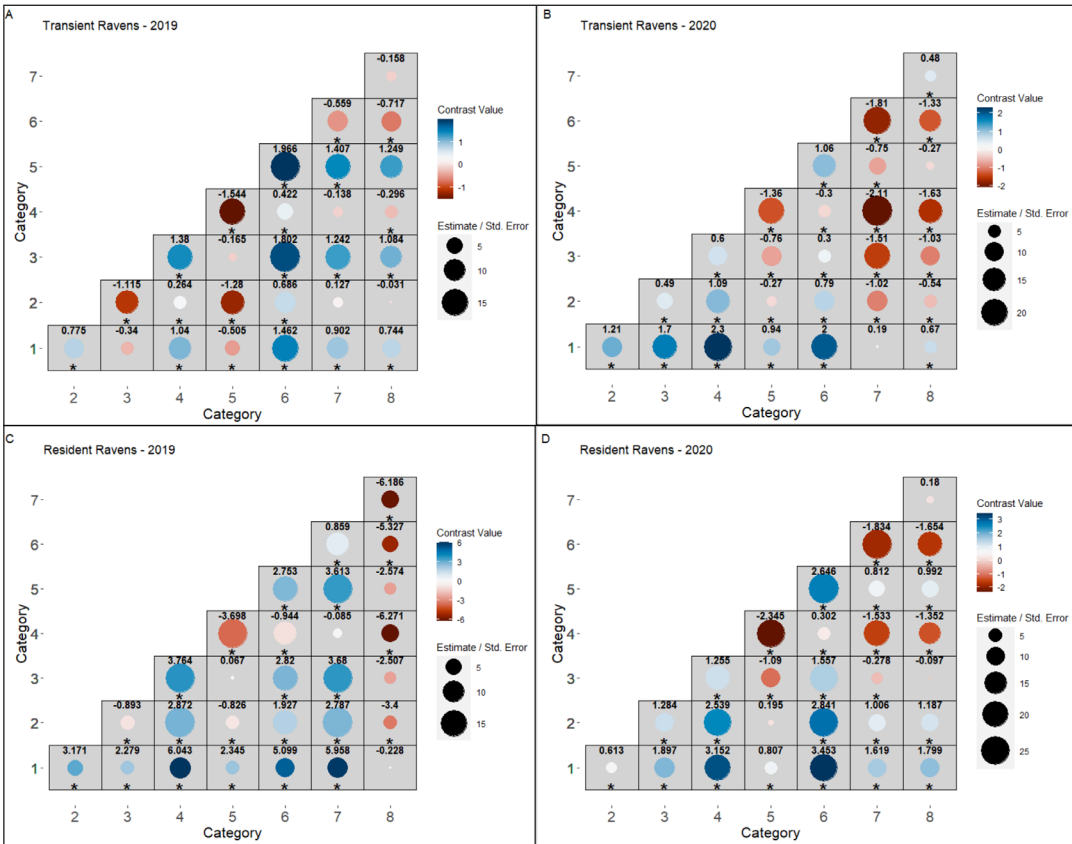
Figure 5. Pairwise contrast estimates of selection coefficients for global positioning system-tracked resident and transient common ravens (*Corvus corax*) monitored in the Great Basin, USA, during 2019 and 2020. Estimates are shown at the top of each tile, while standard error (SE) is represented by size of each circle, and significant contrasts (*P* < 0.05) are denoted with stars in the bottom of each tile. Negative estimates (red) indicate greater selection for the category on the y-axis (relative to the x-axis), while positive estimates (blue) indicate greater selection for the category on the x-axis (relative to the y-axis). Categories represented correspond to quantiles of occurrence and estimated residuals of a linear regression model relating predicted raven occurrence to density, where category 1 = "lowest ψ/low r," category 2 = "lowest ψ/high r," category 3 = "low ψ/low r," category 4 = "low ψ/high r," category 5 = "high ψ/low r," category 6 = "high ψ/high r," category 7 = "highest ψ/low r," category 8 = "highest ψ/high r."

regardless of probability of occurrence) were selected by transients. Contrast analyses revealed that residents generally selected for categories 5 and 7 relative to categories 1 and 2, with the exception of the contrast between categories 5 and 2 (Figure 5). Residents generally showed significant selection for categories with high residuals relative to low residual categories within the same occurrence class, which was somewhat unexpected. For transients, we generally found significantly higher selection for categories 2 and 4 relative to categories 5 and 7 (Figure 5). Transients also showed significant selection for categories with high residuals relative to low residual categories within the same occurrence class.

Discussion

Our occurrence/residual map provides a novel, robust tool that can help to guide management of expanding raven populations in the Great Basin. We used landscape-level patterns of density and occurrence of ravens to obtain meaningful information about raven population structure by evaluating deviations from the expectations of a model predicting raven probability of occurrence (O'Neil et al. 2018*b*) and a model predicting raven density (Coates et al. 2020*b*). We used landscape-level patterns of density and occurrence of ravens to obtain meaningful information about raven population structure by evaluating deviations from the expectations of a model evaluating density as

a function of occurrence. Specifically, we used the residuals from this model to generate hypotheses about the prevalence of breeding and transient ravens across the Great Basin. The resulting maps predicted spatial variation among independent datasets (raven group sizes from point counts and locations of GPS marked individuals) to a moderate extent, suggesting that the spatial pattern in the relationship between density and occurrence can inform characteristics of raven populations at a broad scale across the Great Basin. In some cases, the resulting patterns can indicate relative risk to sensitive species such as sage-grouse (Bui et al. 2010), which may be used to inform management actions.

Several previous studies have demonstrated remarkable differences in sociality, movement patterns, and foraging behavior of ravens depending on breeding status (Webb et al. 2012, Coates et al. 2014, Harju et al. 2018), and the prevalence and composition of anthropogenic food sources (Restani et al. 2001, Marzluff and Neatherlin 2006). Yet, our study may be the first to identify spatially explicit variation in potential population structure across an extensive region. Though our findings should be subject to continued investigation and evaluation, the conservation and management of at-risk species may currently benefit from categorical spatial information that speaks to potential conflict risks associated with raven population structure. Specifically, identifying regions where raven populations have high saturation (i.e., high occurrence and high estimated density; categories 6 and 8) and areas where large proportions of breeding residents are likely (despite relatively lower densities; categories 5 and 7) may represent areas of increased predation pressure on other wildlife species (Bui et al. 2010, Brussee and Coates 2018). By accurately identifying these areas, our map may allow managers and researchers to mitigate impacts of ravens on native species of conservation concern, such as sage-grouse, more effectively.

While our map evaluation analyses indicated that the occurrence/residual map accurately delineated spatial variation in raven population structure across the Great Basin, neither evaluation approach found total agreement between evaluation data and map categorization. For example, we did not find significant differences

in the proportion of large group sizes between categories 3 and 4, although we expected larger proportions in category 4. Additionally, our contrast analysis found that residents generally selected for categories with high residuals (2, 4, 6, 8) over low residuals (1, 3, 5, 7) within the same occurrence category, an unexpected result because we expected residents to select for areas where density was lower than expected given the occurrence. Considering this was the first attempt to empirically describe spatial characteristics of a complex behavioral phenomenon (i.e., the influence of breeding status on territoriality and movement behavior) at a relatively coarse scale, some aberrations from expected trends were not surprising. For example, although we delineate areas predicted to have larger proportions of breeding resident ravens, breeding and territoriality in ravens is a complex ecological process that is in turn dependent on several individual, population, and ecosystem level characteristics such as nest success, population density, or food resource availability (Restani et al. 2001, Kristan et al. 2004, Webb et al. 2012). Further, ravens' behavioral plasticity allows them to readily alter their movement patterns to changing environmental conditions (Bui et al. 2010, Loretto et al. 2017), a trait that almost certainly introduces further variation in our predictions of population structure and our ability to evaluate our map with individual movement data. Despite these potential limitations, the generalized occurrence/residual map successfully predicted variation in group sizes as well as the expected use of different map categories by resident individual ravens relative to transients, suggesting its validity for evaluating raven population structure in the Great Basin.

Our spatially explicit categorical map of population structure provides a useful management and conservation tool that can be applied at broad spatial scales. However, it is important to note that our approach for assessing patterns in density and occurrence did not allow us to incorporate the estimated uncertainty around occurrence and density parameter estimates into our map product. This omission can lead to misinterpretation of trends when the central tendency (in this case, the estimated mean) of an estimated parameter may not be representative of the data due to large or heterogeneous

variance within the data (Cade and Noon 2003). However, given the robustness of the data and analyses used to generate the original occurrence and density maps and the extensive validation analyses we conducted on our map product, we feel confident that our map can be used as a broad management tool in the absence of a more comprehensive study. Indeed, this study was not intended to replace more rigorous, fine scale analyses of raven movement behavior patterns and their influence on predation pressure to native species at local scales. Instead, we have provided a novel tool that provides broad information on raven population structure that may be of use to biologists or managers.

Management implications

Understanding how patterns of raven occurrence and density relate to breeding status, movement behavior, and ultimately foraging success is of critical interest to resource managers tasked with mitigating the impacts of predation from subsidized raven populations on species of conservation concern. Maximizing the efficacy and potential impact of management actions toward accomplishing conservation goals is also a priority for resource managers, who are often limited in scope by logistical, practical, and economic considerations separate from ecological factors. Our map allows for broad inference about spatial variation in predation risk from ravens, which can be used to focus management efforts to regions of high predation risk that overlap with other species ranges. Indeed, we found that nearly half of sage-grouse concentration areas fell in categories where raven population structure (i.e., areas with high concentrations of resident ravens) could be associated with increased predation risk, which could have significant impact on this sensitive species' population growth over time. Our map can also be incorporated in spatially explicit decision support tools (Dettenmaier et al. 2021) to help improve the efficacy of raven management efforts and, ultimately, survival and reproduction of sensitive wildlife species within the Great Basin.

Acknowledgments

Supplemental material

Supplemental material can be viewed at https://digitalcommons.usu.edu/hwi/vol15/iss3/10.

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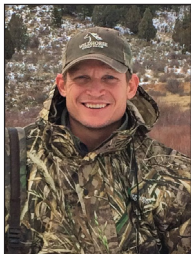
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