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Increased abundance of the common raven within the ranges of greater and Gunnison sage-grouse: influence of anthropogenic subsidies and fire

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Abstract: The common raven (*Corvus corax*; raven) is native to North America and has increased in abundance, especially throughout western North America, during the last century. Human subsidies have facilitated raven dispersal into less suitable habitats and enabled these populations to maintain higher annual survival and reproduction. Concomitantly, overabundant raven populations are impacting other native at-risk species such as the greater sage-grouse (*Centrocercus urophasianus*) and potentially the Gunnison sage-grouse (*C. minimus*). Using Breeding Bird Survey data from 1995–2014, we evaluated raven count data to quantitatively describe changes in abundance and expansion into sagebrush (*Artemisia* spp.) ecosystems, specifically sage-grouse habitat. We focused our analyses on the 7 sage-grouse management zones (MZs) delineated across 11 western U.S. states and 2 Canadian provinces. We assessed the effects of land cover and anthropogenic disturbance on instantaneous growth rate (r) or carrying capacity (K) of ravens. Abundance of ravens in western and southeastern MZs was greater than northeastern MZs within the greater sage-grouse range. While raven abundance was lower in MZ I and II (Alberta, Canada; Dakotas, Montana, and northwestern Colorado, USA; Saskatchewan, Canada; and Wyoming, USA), raven expansion and percent increase were equivalent or greater than all other MZs. High abundance in MZ VII indicated Gunnison sage-grouse have been exposed to increased raven populations for several decades. Areas with greater electric power transmission line density had higher r; higher K was positively related to proportion of urban land cover within 25 km and burned area within 3 km and negatively related to greater distance from landfills and proportion of forest land cover within 15 km. Ravens have capitalized on human subsidies to increase abundance and expand into sagebrush ecosystems that did not historically support high raven populations. As such, managers are now faced with a new dilemma of reducing populations of a native species to benefit other native sagebrush obligate species.

Key words: anthropogenic subsidies, *Centrocercus minimus*, *Centrocercus urophasianus*, common raven, *Corvus corax*, fire, greater sage-grouse, Gunnison sage-grouse, human–wildlife conflict, native invader, N-mixture model, population growth, subsidized predator, synanthropic behavior

During the last century, distribution and abundance of common ravens (*Corvus corax*; ravens) have increased throughout western North America (Sauer et al. 2017, Harju et al. 2021). Leu et al. (2008) associated this phenomenon with the expansion of the human footprint, suggesting ravens' synanthropic behavior enabled them to exploit human resources that increased their fitness. Regions such as the Mojave Desert (Boarman 1993) and Alaska's North Slope, USA (Backensto 2010) were much less habitable or uninhabitable by ravens prior to human development; thus, the capacity of areas to support ravens within their historical range has increased with increasing infrastructure to sustain humans (Leu et al. 2008; Figure 1).

Ravens utilize low and high-voltage electric power transmission lines as safe nesting or roosting locations and as effective perch locations (Engel et al. 1992*b*, Boarman 1993, Knight and Kawashima 1993, Steenhof et al. 1993, Coates et al. 2014*a*, Howe et al. 2014, Gibson et

Figure 1. Common ravens (*Corvus corax*) nesting on power pole in eastern Oregon, USA (*photo courtesy of L. Perry*).

Figure 2. Common ravens (*Corvus corax*) at Baker County landfill south of Baker City, Oregon, USA (*photo courtesy of L. Perry*).

al. 2018, O'Neil et al. 2018, Coates et al. 2020). Agricultural irrigation structures have provided safe roosting locations for communally roosting ravens (Littlefield and Ivey 1994, Perry et al. 2021). Tall, durable structures such as billboards, windmills, oil and gas wells, polebarns, highway overpasses, water tanks, and other industrial structures provide safety from predators, vantage points for hunting/foraging, and overwinter shelter (Larsen and Dietrich 1970, White and Tanner-White 1988, Steenhof et al. 1993, Peebles and Conover 2017), and ravens often select many of these structures to support their nests (Kristan and Boarman 2007, Coates et al. 2014*b*, Howe et al. 2014, Gibson et al. 2018, Harju et al. 2018). In south-central Wyoming, USA, Harju et al. (2018) documented 96–100% of raven nests were located on infrastructure, and proximity of raven nests to anthropogenic subsidies has been reported to increase juvenile survival (Webb et al. 2004).

Available food subsidies for ravens have also increased with the human footprint in various forms. The number of campgrounds and human presence in the western United States have provided important food resources to ravens, resulting in greater relative abundance and higher reproductive rates of ravens near campgrounds, settlements, and roadside rest areas and higher reproduction rates in ravens (Marzluff and Neatherlin 2006, Leu et al. 2008, O'Neil et al. 2018). These oases typically provide a water source and abundance of food items, such as trash, fishing discards, and offal piles from hunter-killed wildlife (Oro et al. 2013). Not only are they a dense source of sustenance, they are also persistent resources that can be relied on over time. In the same way, ravens have learned to rely on and exploit landfills for food resources (Restani et al. 2001, Boarman et al. 2006, Peebles and Conover 2017). Landfills provide an abundant and continual source of food with almost no harassment from predators or people (Figure 2). Ravens can also be found foraging for insects, rodents, and/or grains on crop fields (Engel and Young 1992*a*, O'Neil et al. 2018, Coates et al. 2020). Less frequently, but with potentially larger financial impacts, ravens depredate newly born lambs (*Ovis aries*) or calves (*Bos taurus*) on livestock ranches (Larsen and Dietrich 1970, Coates et al. 2016*a*, Boarman and Heinrich 2020). Finally, road networks provide increased food availability in the form of roadkill, which are scavenged by ravens (Kristan et al. 2004).

Human subsidies have enabled ravens to access and utilize a broader spectrum of ecosystems by improving habitat quality for ravens across a larger spatial footprint in western North America. This expansion into previously unsuitable habitat has resulted in higher numbers of ravens (Coates et al. 2016*a*, Peebles et al. 2017, Sauer et al. 2017, Coates et al. 2020), making ravens an overabundant native species in many parts of western North America. Subsidized ravens have impacted Steller's jays (*Cyanocitta stelleri*) and likely contributed to low reproduction in marbled murrelets (*Brachyramphus marmoratus*; Peery and Henry 2010), least terns (*Sterna antiliarum*; Avery et al. 1995), black-crowned night-herons (*Nycticorax nycticorax*; Brussee et al. 2016), and federally listed snowy plovers (*Charadrius nivosus*; Dinsmore et al. 2014; Ellis et al. 2015, 2020; Lau et al. 2021). Additionally, ravens have been shown to be an effective predator on prey of conservation concern, including juvenile desert tortoises (*Gopherus agassizii*; Boarman 2003, Kristan and Boarman 2003) and the eggs of greater sage-grouse (*Centrocercus urophasianus*; Coates and Delehanty 2008, Lockyer et al. 2013, Taylor et al. 2017). Such prey species have not previously been exposed to high raven abundance and now may be more vulnerable to raven depredation.

Robust assessments to identify and measure the contribution of human subsidies and habitat condition are necessary to fully understand the mechanisms influencing raven population growth. This is especially critical to address conservation of numerous sensitive species and the continued range expansion and population growth of ravens. Both greater and Gunnison sage-grouse (*C. minimus*) populations have declined in abundance and distribution (Schroeder et al. 2004, Gunnison Sage-Grouse Rangewide Steering Committee 2005, Garton et al. 2011, Nielson et al. 2015). These species declines have resulted in unprecedented large spatial scale conservation and management activities to avert the species being listed for protection under the U.S. Endangered Species Act (Western Association of Fish and Wildlife Agencies 2015).

Population growth of native invaders, such as the raven in some ecosystems, is not restricted by naturally occurring resources because these species often rely on subsidized resources provided by humans (Carey et al. 2012, Oro et al. 2013). When this occurs, annual survival and reproduction are not limiting these species, which can lead to hyperpredation rates on prey species in areas where generalist predators have greater abundance than natural carrying capacity would allow (Oro et al. 2013). For example, greater sage-grouse nest success (Coates and Delehanty 2010, Dinkins et al. 2016, Gibson et al. 2018, Kohl et al. 2019, Coates et al. 2020) and lek trends have been negatively associated with ravens (Peebles et al. 2017, Gibson et al. 2018). Meanwhile, no formal assessment of raven influence on Gunnison sage-grouse exists. Thus, we sought to fill knowledge gaps related to if and how raven abundance has changed in greater and Gunnison sage-grouse habitat. To accomplish this, we evaluated population trends of ravens throughout the ranges of greater and Gunnison sage-grouse. This research included comparisons of the factors influencing instantaneous growth rate (r) and carrying capacity (K) and relative raven abundance among 7 sage-grouse management zones (MZs). We hypothesized that increased anthropogenic structures for perching, nesting, and/or roosting (hereafter, perch structures) and food subsidies near anthropogenic features would provide the means for ravens to expand in number and have increased r. Thus, we predicted perch structures (transmission lines, oil and gas wells, and wind power infrastructure) and food subsidy areas (cropland, landfills, roads, and urban areas) would be positively connected to r or K (contributing to greater abundance). In addition, we hypothesized that increased tree expansion and area burned across time would also be positively related with r or K by providing ravens perching substrate and increased foraging opportunities in areas fragmented by fire.

Study area

Our study area spanned portions of 11 U.S. states and 2 Canadian provinces and included a mix of private and public lands in sagebrush (*Artemisia* spp.) ecosystems. The study area boundary encompassed a 25-km buffer around the greater and Gunnison sage-grouse distributions defined by Schroeder et al. (2004) and fell within the 7 MZs identified by the Western Association of Fish and Wildlife Agencies, Conservation Strategy for Greater Sage-Grouse (Stiver et al. 2006; Figure 3). Each MZ corresponds to a major floristic province (Miller and Eddleman 2001) and EPA level III ecoregions (Wilken et al. 2011). The Western Association of Fish and Wildlife Agencies used floristic provinces instead of political boundaries to delineate MZs based on ecological, biological, and environmental consistency and subsequent response to management actions that align with simi-

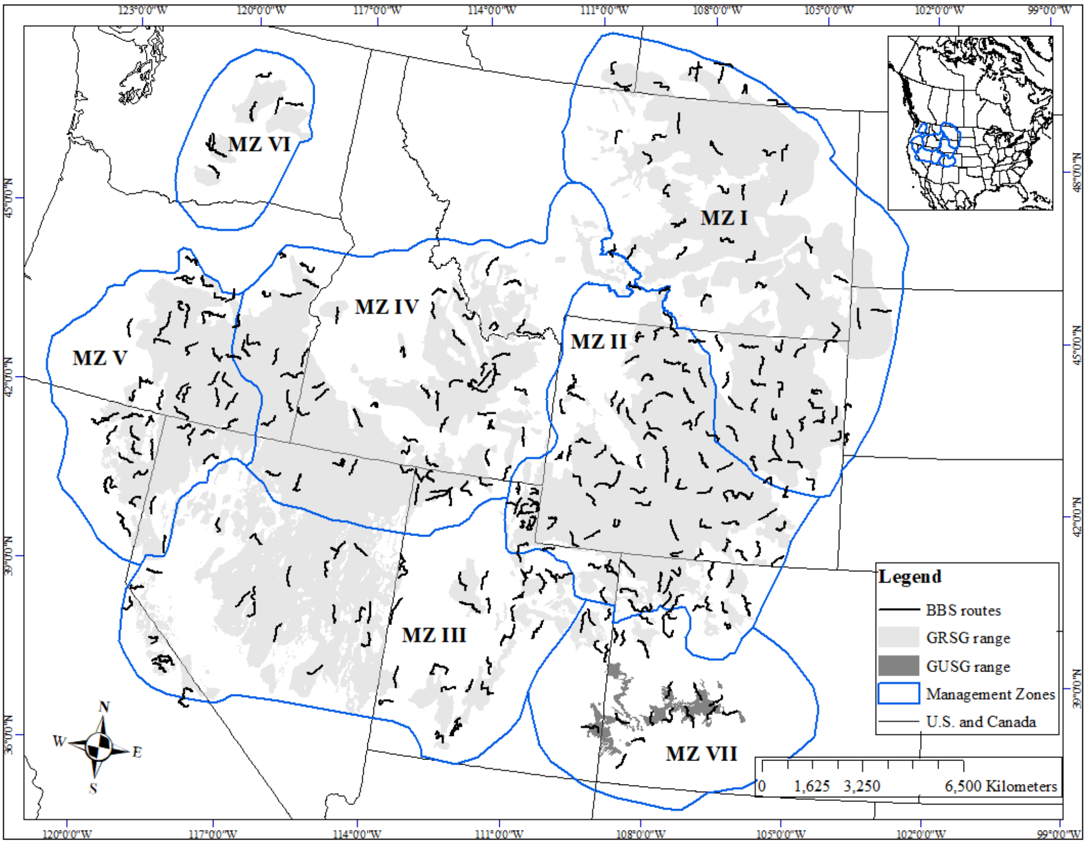

Figure 3. Study area map inclusive of sage-grouse management zones (MZ) I–VII and range extents of greater (*Centrocercus urophasianus*; GRSG) and Gunnison (*C. minimus*; GUSG) sage-grouse. Inset map of North America indicating study area extent. Common raven (*Corvus corax*) count data were compiled from 1996–2014 along 358 Breeding Bird Survey routes within 25 km of greater or Gunnison sage-grouse ranges.

lar vegetation communities used as habitat by sage-grouse populations (Stiver et al. 2006).

Big sagebrush (*A. tridentata*) dominated sage-grouse habitat in each MZ; however, the subspecies of big sagebrush (basin [*A. t. tridentata*], mountain [*A. t. vaseyana*], and Wyoming [*A. t. wyomingensis*]) and other sagebrush species (e.g., black [*A. nova*] and silver [*A. cana*]) providing habitat to sage-grouse varied within and between MZs depending on factors including climate, soils, latitude, and topography (Wilken et al. 2011). Descriptions of variation in common shrub and herbaceous plant species across the 7 MZs have been detailed in Brooks et al. (2015). The primary human land use in all MZs was livestock grazing. Anthropogenic development differed across our study area with eastern and western MZs having sporadically located towns, cities, mining, agricultural conversion, and wind power, whereas eastern MZs also included areas of oil and gas development.

Methods

To evaluate changes in raven abundance, instantaneous growth rate, and carrying capacity, we compiled Breeding Bird Survey (BBS) data from 1995–2014. Data from BBS represented the total number of ravens detected along 39.4-km survey routes during each breeding season (primarily May to June; Ziolkowski et al. 2010, Pardieck et al. 2016). For each BBS survey route, the number of ravens was quantified within 0.4 km of 50 stop locations spaced 0.8 km apart, where observers stopped to conduct 3-minute point counts (Ziolkowski et al. 2010, Pardieck et al. 2016).

We quantified predictor variables describing anthropogenic and landscape characteristics from readily available geographical information system (GIS) datasets (Table 1). Variable data sources and raw data pixel sizes are described in Table 1. We calculated and extracted these predictor variables relative to BBS routes using

Table 1. Descriptions of predictor variables with associated data source used in open population N-mixture models evaluating common raven (*Corvus corax*) Breeding Bird Survey (BBS) trends, 1995–2014. Predictor variables were quantified within 3, 8, 15, and 25-km buffers around BBS survey routes or were calculated as distance variables. However, precipitation variables were quantified as total precipitation within 10 km of a BBS route. Data were collected from 11 U.S. states and Alberta and Saskatchewan, Canada.

Predictor variable	Description	Resolution	Data source
Anthropogenic			
Distance to town	Average distance to a town >10,000 people	30 m	U.S. Baruch Geoportal and Canada AltaLIS and GeoSask
Human population density	Annual density (no./km^2) quantified by U.S. or provincial county	U.S. county or provincial	U.S. Census Bureau and Canadian CANSIM (1995–2014)
Landfill	Average distance to a landfill	Point	SAGEMAP and hand digitization
Oil and gas density	Annual density of oil and gas wells (no./km^2)	Point	State oil and gas commissions (1990–2014)
Power line density	Density of transmission lines	Line	U.S. Energy Information Administration and Canada AltaLIS
Proportion cropland	Proportion of spatial buffer classified as cultivated cropland during 3 timeframes centered on 2000, 2005, and 2010	300 m	European Space Agency Climate Change Initiative (SPOT)
Proportion urban	Proportion of spatial buffer classified as urban land cover during 3 timeframes centered on 2000, 2005, and 2010	300 m	SPOT (2000, 2005, 2010)
Roads and rail density	Density of roads and railroads (km/km^2)	Line	U.S. Census Bureau TIGER and Statistics Canada Road Network
Wind turbine density	Annual density of wind turbines (km/km^2)	Point	U.S. Geological Survey and Natural Resources Canada Wind Resource (1990–2014)
Land cover			
Burned area	Annual proportion of area burned	30 m	Monitoring Trends in Burn Severity (MTBS; 1990–2014; Eidenshink et al. 2007)
Forested	Proportion of all conifer-dominated land cover types during 3 timeframes centered on 2000, 2005, and 2010	300 m	SPOT (2000, 2005, 2010)
Shrubland	Proportion of all shrubland-dominated land cover types during 3 timeframes centered on 2000, 2005, and 2010	300 m	SPOT (2000, 2005, 2010)
Precipitation			
Spring precipitation	Annual total precipitation (mm) March to May within 10 km	1,000 m	Daymet (1994–2014)
Spring snow water equivalent (SWE)	Annual SWE (kg/m^2) March to May within 10 km	1,000 m	Daymet (1994–2014; Thornton et al. 1997, 2014)
Summer precipitation	Annual total precipitation (mm) July to August within 10 km	1,000 m	Daymet (1994–2014; Thornton et al. 1997, 2014)
Winter precipitation	Annual total precipitation December to February (mm) within 10 km	1,000 m	Daymet (1994–2014; Thornton et al. 1997, 2014)
Winter snow water equivalent	Annual SWE (kg/m^2) December to February within 10 km	1,000 m	Daymet (1994–2014; Thornton et al. 1997, 2014)

ArcMap version 10.2 (ESRI, Redlands, California, USA), Geospatial Modeling Environment version 0.7.3.0 (http://www.spatialecology.com/gme), or the "raster" package version 2.3-40 in R version 3.0.2 (R Development Core Team 2021). In summary, we quantified GIS data representing distance to towns and cities, landfills, and transmission lines; density of human population, major and gravel roads (inclusive of railroads), oil and gas wells, transmission lines, and wind turbines; proportion of land cover as cropland, forested, shrubland vegetation, and urban; and proportion burned vegetation.

We initially obtained locations of landfills that we used to calculate distance and density variables from SAGEMAP (Knick and Schueck 2002). However, the SAGEMAP landfill product did not include landfill locations in Canada; thus, we added landfill locations for southern Alberta and Saskatchewan manually. Density and proportion predictor variables were quantified as average values within 3, 8, 15, and 25-km buffers around BBS routes. We selected these spatial extents to represent potential raven attraction to resources based on daily and seasonal movement of breeding and nonbreeding ravens (Peebles and Conover 2017, Harju et al. 2018, Boarman and Heinrich 2020, Coates et al. 2020).

To acquire seamless land cover (vegetation and urban) data across southern Canada and the western United States, we obtained land cover variables from the European Space Agency (ESA 2017), which had a 300-m resolution (ESA 2017). We used total fire footprint data from the Monitoring Trends in Burn Severity (MTBS; Eidenshink et al. 2007) database to calculate fire proportion variables. Fire proportion variables were cumulative across time, which we thought generally represented the effects of fire on big sagebrush vegetation communities that have recovery times of 25–35 years in mountain big sagebrush communities and 50–120 for Wyoming big sagebrush communities (Baker 2006, 2011).

To assess potential weather effects on instantaneous growth rate, we quantified winter precipitation, spring precipitation, summer precipitation, spring snow water equivalent (SWE), and winter SWE from Daymet (Thornton et al. 1997, Thornton et al. 2014). We calculated precipitation and SWE variables at only 1 spatial scale as the total accumulation within 10 km of each BBS survey route. This was intended to simplify our modeling process because seasonal weather patterns were spatially correlated at large spatial extents. Daily precipitation and SWE were acquired from Daymet as daily precipitation (mm) and SWE ($kg/m^{2)}$, and we then summed daily precipitation for spring (March to May), summer (June to August), and winter (December to February) and averaged SWE for spring (March to May) and winter (December to February).

Detection probability variables

Detection probability was assessed as variables describing differences in conditions while observers were conducting BBS surveys. We did not include quantifications of landscape characteristics influencing detection of ravens because the BBS count data was from 50 stop locations along each survey route. Additionally, BBS protocols only allowed ravens within 0.4 km of the observer to be recorded. Variables describing detection probability included observer experience, number of observers, mean temperature, and mean wind speed, which were all reported in the BBS database. We reclassified the BBS observer experience data to a binary variable of experienced versus novice observers by contrasting first field season versus >1 field season. We also reclassified the number of observers from BBS to be a binary variable contrasting surveys conducted with a single person versus an observer with an assistant.

Data analysis

To evaluate raven trends within sage-grouse habitat, we used open population N-mixture models to assess differences in raven numbers and population growth from 1995 to 2014 (Royle 2004, Dail and Madsen 2011, Hostetler and Chandler 2015). We conducted our analyses in the unmarked package (version 0.11-0) in R using the pcountOpen function (Fiske and Chandler 2011). First, we determined the best distribution for our data as either Poisson or negative binomial, then compared no trend, exponential growth, and density-dependent population growth (Gompertz and Ricker) model structures (Hostetler and Chandler 2015). The distribution and model structure with the lowest Akaike's information criterion (AIC) and highest Akaike weights (w_i; Burnham and Anderson 2002) was considered our null model. We compared our null model to models including covariates describing initial abundance (Λ; year = 1995), population growth (instantaneous growth rate [r] or maximum per capita rate of increase [λ]), and equilibrium abundance (K; Hostetler and Chandler 2015). Equilibrium abundance was analogous to carrying capacity, and we only included it in additive modeling when the best model structure was Gompertz or Ricker density-dependent growth. Density-dependent growth would indicate that raven counts across time were dependent on the number of ravens at a BBS route the year prior.

Surveys for BBS were conducted as single counts per year with assumed equal detection based on distance to observed ravens. However, BBS routes included observation-related data (e.g., observer experience, number of observers, temperature, and wind speed) that we assessed as potential factors influencing observers' ability to detect a raven during BBS surveys. Each year, many annual BBS routes do not get surveyed, leading to missing annual count data, which pcountOpen handles by modeling counts across time from the spatiotemporal count data that does exist. To allow BBS routes to inform models, each route within our study area needed to either have a count during the initial year or at least 1 instance of sequential annual counts to allow growth to be calculated between those years (Hostetler and Chandler 2015).

Covariates describing Λ focused on describing how raven counts differed across space in 1995, whereas covariates describing r or K described how covariates influenced raven counts across space and time. We assessed MZ as a predictor of Λ to describe large-scale differences of raven abundance across the ranges of greater and Gunnison sage-grouse stratified by the 7 MZs. We also assessed all land cover, density, and distance variables as predictors of Λ by aligning the value of these variables to BBS counts from 1995. For static variables, such as landfills, roads, and transmission lines, there was only 1 value for each of these variables across time; thus, we assessed the single value of these variables for each BBS route as a potential predictor of Λ, r, and K of ravens across space. We evaluated time-varying variables as predictors of r and K. We quantified proportion burned and human population, oil and gas well, and wind turbine densities as time-varying variables and aligned them annually to BBS route data as the variable value from 1 year prior and 3 years prior (3-year lag) to each BBS survey count. Land cover variables from SPOT datasets (cropland, forested, and urban proportions) were only available as 5-year timespans centered at a median year (1997–2002, 2003–2007, 2008–2012); thus, we aligned these variables to each annual BBS count to the closest 5-year time span.

We generated Pearson's correlation matrices to assess whether predictor variables had potential multicollinearity. If any 2 predictor variables had correlation coefficient $>|0.65|$, then we did not allow those 2 variables to be included in the same part of N-mixture models (e.g., no 2 correlated variables were included as predictors of Λ). Prior to additive modeling with multiple predictor variables, all predictor variables for Λ, r, and K were tested as single variable models to identify uninformative variables based on recommendations from Arnold (2010). We removed uninformative predictor variables with 85% confidence intervals (CI) that overlapped zero from further modeling. We compared all combinations of additive models with informative predictor variables on Λ, r, or K with AIC and w_i. We estimated raven trends with 95% CI across time from the model with the lowest AIC and greatest w_i using empirical Bayes methods within the unmarked package (Fiske and Chandler 2011). This was reported as the average number of ravens per BBS route across our study area stratified by MZ.

Results

We quantified raven abundance from 358 BBS routes throughout 7 MZs (66 in MZ I, 96 in MZ II, 53 in MZ III, 63 in MZ IV, 48 in MZ V, 8 in MZ VI, and 24 in MZ VII; Figure 3). Our analyses included 20 years of counts; however, only 13.7% (49) of the BBS survey routes were monitored every year of our study duration. There were 4,706 total annual BBS surveys conducted and 2,454 missing annual surveys. This resulted in 165 (46.1%) routes with >15 surveyed years, 258 (72.1%) routes with >10 surveyed years, and 327 (91.3%) routes with >5 surveyed years. With the exception of 2 BBS routes, all other

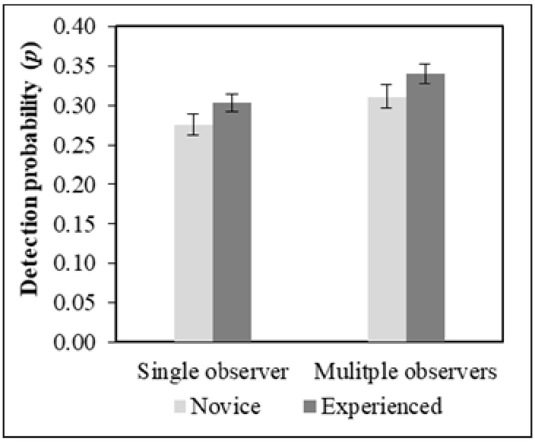

Figure 4. Estimated detection probability based on categorized number of observers and their level of experience. We compared surveys with single versus multiple observers (>1 observer) and novice versus experienced observers (>1 year conducting Breeding Bird Survey routes).

routes included in our analyses had at least 1 instance of sequential annual surveys. This allowed calculation of growth at least once across our study duration. The 2 exception routes had the single annual count during the initial year (1995), which informed the part of our models related to initial abundance.

The best distribution and population growth structure for our models was negative binomial with Gompertz density-dependence, which was 42.92 AIC points lower than the next best population growth structure model. Detection probability was best described by the observer's experience and number of observers based on lowest AIC among competitive models with single and additive covariates describing potential differences in detection probability. However, the second AIC-ranked model of detection probability covariates was a model that included observer experience, number of observers, and average wind speed with ΔAIC = 1.22. The third AIC-ranked model of detection probability had ΔAIC = 9.11 compared to the top model. Wind speed was negatively associated with detection probability (parameter estimate = -0.05, 95% CI: -0.07 to -0.03), but we excluded this parameter based on parsimony for all other models with covariates on Λ, r, and K. Surveys conducted by experienced observers (>1 season experience) and with 2 people (observer with an assistant) had higher detection probability compared to novice observers and surveys with a single observer (Figure 4).

After inclusion of covariates on Λ, r, and K, our top 4 AIC-selected models had individual parameter estimates that were stable between single variable and additive models, indicating multicollinearity was not an issue. Our top and second AIC-selected models included MZ and proportion burned area within 3 km ($\text{Burn}_{3\text{km}}$) as predictors of Λ and average distance to a landfill (Landfill) and proportions of urban land cover within 25 km ($\text{Urban}_{25\text{km}}$), forested land cover within 15 km ($\text{Tree}_{15\text{km}}$), and a 3-year lag for burned area within 3 km ($\text{Burn}_{3\text{kmL3}}$) as predictors of K (Table 2). There was some model uncertainty among the top 4 models, which were within 4 ΔAIC and contained 0.91 of the cumulative w_i (Table 2). We primarily report results from the model with the lowest AIC because this model was the most parsimonious and had $w_i = 0.40$ (Table 2). The second AIC-selected model included 1 additional covariate (density of transmission lines within 15 km [$\text{Power}_{15\text{km}}$]) compared to the top AIC-selected model. All models equating to cumulative 1.00 w_i included MZ as a predictor of Λ (Table 2). Our results indicated that Λ was greatest in southern and western MZs in 1995, and BBS routes with greater proportion burned area within 3 km had more ravens counted in 1995, although the effect of burned area was slightly different depending on MZ (Figure 5). For the second AIC-selected model, density of transmission lines within 15 km ($\text{Power}_{15\text{km}}$) was positively related to r (Figure 6); however, the effect of $\text{Power}_{15\text{km}}$ was slightly imprecise (parameter estimate = 0.64; 95% CI: -0.33 to 1.62). For the top AIC-selected model, $\text{Burn}_{3\text{kmL3}}$ and $\text{Urban}_{25\text{km}}$ were positively related to K (Figures 7B and 7D, respectively), and Landfill and $\text{Tree}_{15\text{km}}$ were negatively related to K (Figures 7A and 7C, respectively).

Our results show that raven numbers increased throughout greater and Gunnison sage-grouse habitat and much of the sagebrush ecosystem during our 20-year study period (Figure 8A). The increase in raven numbers per BBS route was primarily in the form of increased K across time, but we also found an imprecise effect of r in areas with more transmission lines. In general, numbers of ravens per BBS route increased to the highest numbers per BBS route in MZ III–VII in 2014 (Figure 8). This corresponded to those southern and west-

Table 2. Model selection rankings for the top 10 open population N-mixture models that evaluated common raven (*Corvus corax*; raven) trends with Gompertz density-dependent population growth, 1995–2014. These models included management zone (MZ) and proportion burned area within 3 km (Burn$_{\text{3km}}$) during 1995 as predictors of initial abundance (Λ); power line density within 15 km (Power$_{\text{15km}}$) of a predictor of instantaneous growth rate (r); and distance to landfill (Landfill) and time-varying proportion of land cover classified as urban within 25 km (Urban$_{\text{25km}}$), forested within 15 km (Tree$_{\text{15km}}$), and burned area within 3 km (Burn$_{\text{3kmL3}}$) as predictors of carrying capacity (K). For K, the proportion of burned area covariate fit the data best aligned with a 3-year lag. All models included detection covariates contrasting the experience of the observer and the number of observers. Raven count data were compiled from Breeding Bird Survey route data (Ziolkowski et al. 2010, Pardieck et al. 2016).

Models[a]	Parameters	AIC	ΔAIC	w_i
Λ(MZ+Burn$_{\text{3km}}$)+r(.)+K(Landfill+Burn$_{\text{3kmL3}}$+Tree$_{\text{15km}}$+Urban$_{\text{25km}}$)	18	34,536.34	0.00	0.40
Λ(MZ+Burn$_{\text{3km}}$)+r(Power$_{\text{15km}}$)+K(Landfill+Burn$_{\text{3kmL3}}$+Tree$_{\text{15km}}$+ Urban$_{\text{25km}}$)	19	34,536.90	0.56	0.31
Λ(MZ)+r(.)+K(Landfill+Burn$_{\text{3kmL3}}$+Tree$_{\text{15km}}$+ Urban$_{\text{25km}}$)	17	34,538.89	2.55	0.11
Λ(MZ)+r(Power$_{\text{15km}}$)+K(Landfill+Burn$_{\text{3kmL3}}$+Tree$_{\text{15km}}$+Urban$_{\text{25km}}$)	18	34,539.43	3.09	0.09
Λ(MZ+Burn$_{\text{3km}}$)+r(Power$_{\text{15km}}$)+K(Landfill+Burn$_{\text{3kmL3}}$+Tree$_{\text{15km}}$)	18	34,541.45	5.11	0.03
Λ(MZ)+r(Power$_{\text{15km}}$)+K(Landfill+Tree$_{\text{15km}}$+ Urban$_{\text{25km}}$)	17	34,542.04	5.70	0.02
Λ(MZ+Burn$_{\text{3km}}$)+r(Landfill)+K(Burn$_{\text{3kmL3}}$+Tree$_{\text{15km}}$+Urban$_{\text{25km}}$)	18	34,542.86	6.52	0.02
Λ(MZ)+r(Power$_{\text{15km}}$)+K(Landfill+Burn$_{\text{3kmL3}}$+ Tree$_{\text{15km}}$)	17	34,544.01	7.67	0.01
Λ(MZ)+r(Landfill)+K(Burn$_{\text{3kmL3}}$+Tree$_{\text{15km}}$+ Urban$_{\text{25km}}$)	17	34,545.26	8.92	0.00
Λ(MZ+Burn$_{\text{3km}}$)+r(Power$_{\text{15km}}$)+K(Urban$_{\text{25km}}$+Tree$_{\text{15km}}$ +Burn$_{\text{3kmL3}}$)	18	34,546.03	0.00	0.00

[a] AIC for our null model = 34,854.73 (ΔAIC = 318.39) including negative binomial distribution and Gompertz density-dependence growth structure. AIC = 34,799.58 (ΔAIC = 263.24) for the null model with experience and number of observers on detection probability.

ern MZs with greater Λ; thus, areas with high numbers of ravens continued to elevate. These increases indicated 1.4 (MZ III), 1.7 (MZ IV), 1.5 (MZ V), and 4.1 times (MZ VI) more ravens over 20 years. While MZ I and II had relatively lower abundance, patterns in eastern and northern greater sage-grouse habitat indicated increased abundance with 3.3 and 2.1, respectively, times as many ravens in 2014 as compared to 1995 (Figure 8). The low abundance in 1995 in MZs I and II meant ravens expanded into previously unoccupied areas of greater sage-grouse habitat. Gunnison sage-grouse habitat was approximately half the surveyed area in MZ VII, which nearly had twice (1.8 times) as many ravens per BBS route by the end of the survey period.

Discussion

Using BBS data, we evaluated raven trends to quantitatively describe their expanding abundance in sagebrush ecosystems, specifically greater and Gunnison sage-grouse habitat. Overall patterns from 1995 to 2014 indicated raven abundances were greatest and increasing in the western and southeastern MZs (III, IV, V, VI, and VII) but began to expand farther northeast throughout the remaining MZs (I and II), which were the only MZs with relatively low abundance of ravens (Figure 8). This pattern supports similar findings from Harju et al. (2021). Our results also highlight the ability of ravens to capitalize on human subsidies (landfills, transmission power lines, and urban land cover) and provide novel insights regarding higher abundance and increasing K in parts of the sagebrush ecosystem that have been burned. While most areas included in our analyses show annually increasing numbers of ravens, there was expansion in spatial area used by ravens across MZs. This was most apparent in MZs I and II, where 16 (24%) and 2 (2.1%), respectively, of BBS routes started with zero counted ravens in 1995 but had counts greater than zero by 2014. Interestingly, MZ I was the only MZ with BBS routes (27 [40.9%]) that never had a raven counted across the 20-

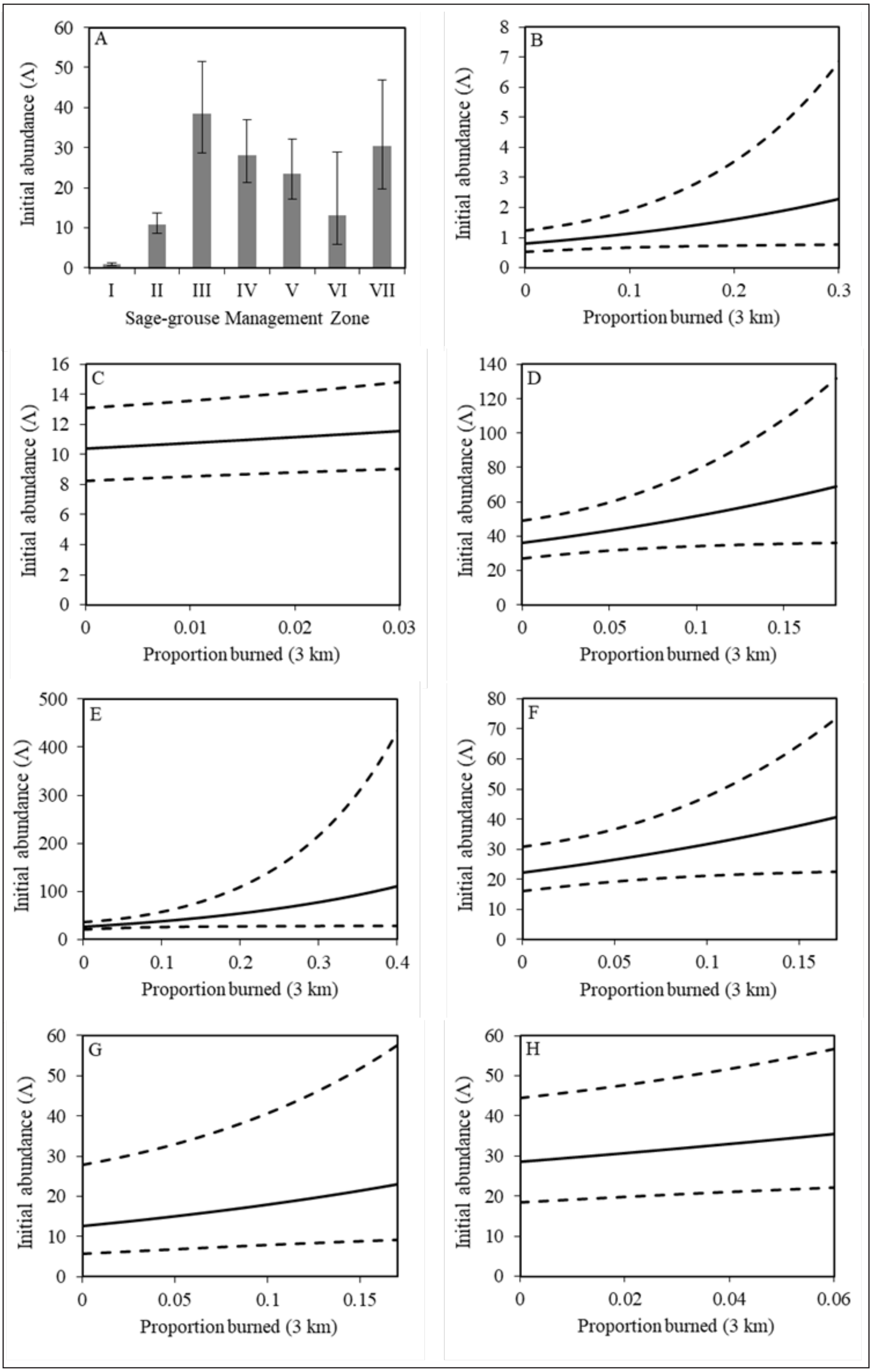

Figure 5. Predicted differences in Λ (1995) of common ravens (*Corvus corax*; ravens) among management zones (MZs; A) and effect of proportion of burned areas within 3 km of a Breeding Bird Survey (BBS) route for MZ I (B), MZ II (C), MZ III (D), MZ IV (E), MZ V (F), MZ VI (G), and MZ VII (H). Predictions based on top ΔAIC open population N-mixture model. Raven count data were compiled from 1996–2014 along 358 BBS routes within 25 km of the greater (*Centrocercus urophasianus*) or Gunnison (*C. minimus*) sage-grouse ranges.

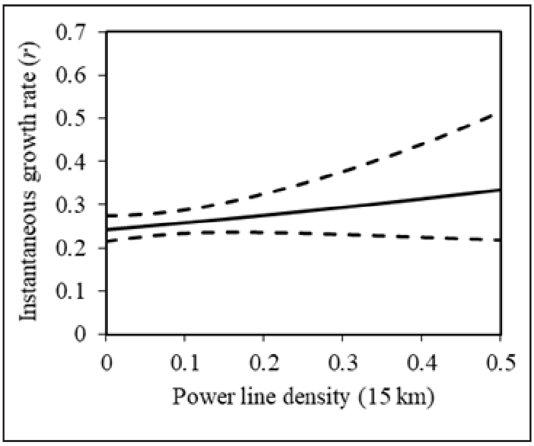

Figure 6. Predicted effect of power line density within 15 km of a Breeding Bird Survey (BBS) route on instantaneous growth rate (*r*) from second AIC-selected open N-mixture model. Common raven (*Corvus corax*) count data were compiled from 1996–2014 along 358 BBS routes within 25 km of the greater (*Centrocercus urophasianus*) and Gunnison (*C. minimus*) sage-grouse ranges.

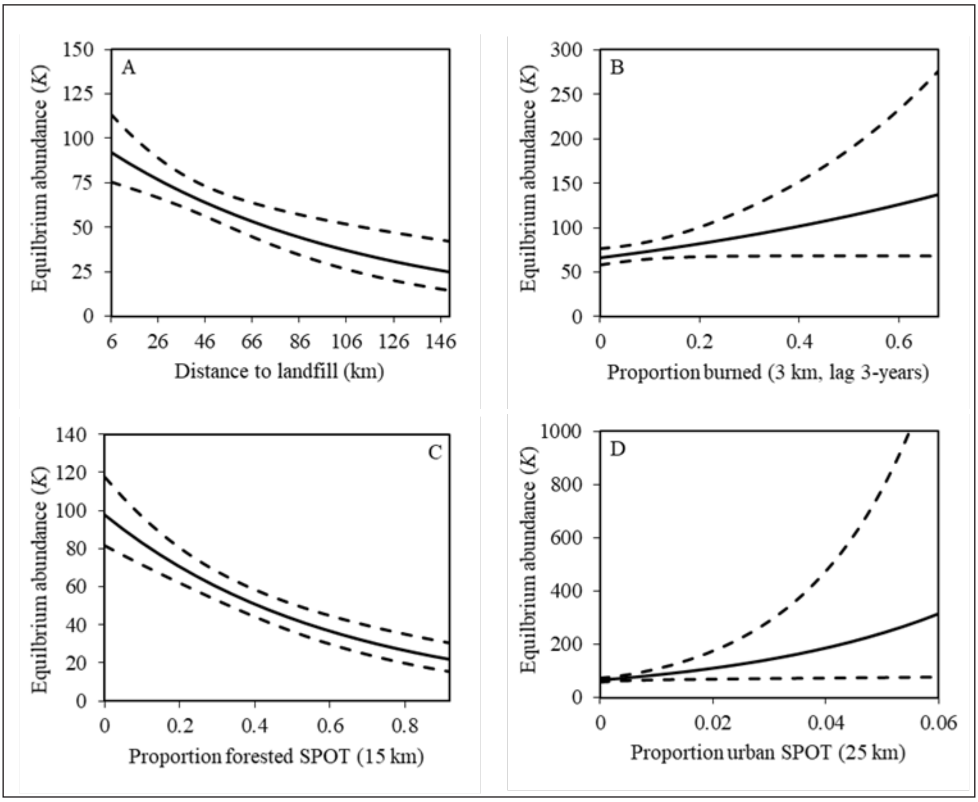

Figure 7. Predicted effects of distance to landfill (A) and proportion of burned (within 3 km [B]), forested (within 15 km [C]), or urban land cover (within 25 km [D]) on equilibrium abundance (*K*; carrying capacity) from top AIC-selected N-mixture model. Common raven (*Corvus corax*) count data were compiled from 1996–2014 along 358 Breeding Bird Survey routes within 25 km of the greater (*Centrocercus urophasianus*) and Gunnison (*C. minimus*) sage-grouse ranges.

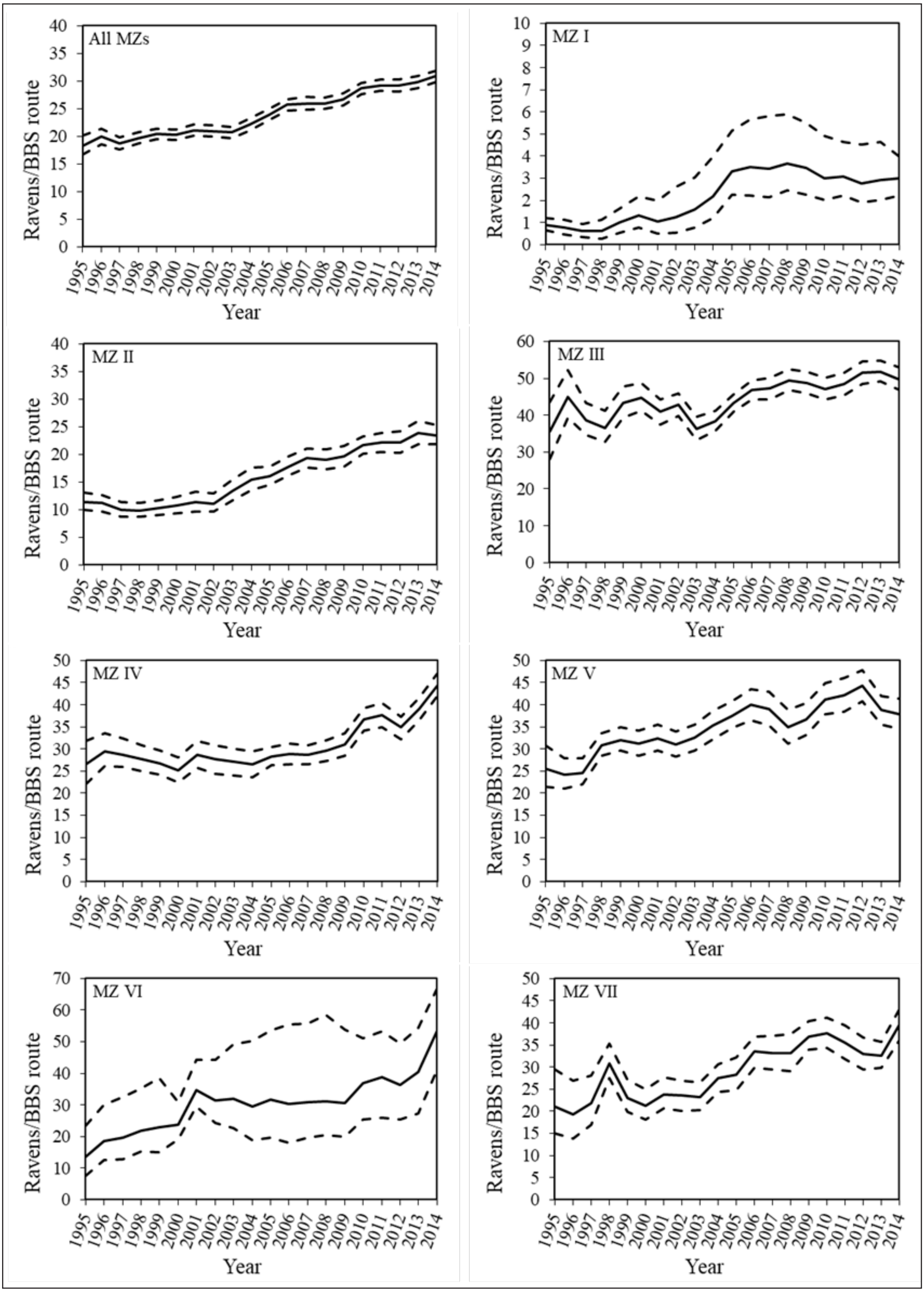

Figure 8. Predicted average common raven (*Corvus corax*; raven) counts per Breeding Bird Survey (BBS) route, 1996–2014, from N-mixture models stratified by 7 sage-grouse management zones (MZs). We report overall average raven counts per BBS route, MZ I, MZ II, MZ III, MZ IV, MZ V, MZ VI, and MZ VII. Predicted counts and 95% confidence intervals were generated using empirical Bayes methods. Raven counts for models were obtained from BBS route data within 25 km of the greater (*Centrocercus urophasianus*) and Gunnison (*C. minimus*) sage-grouse ranges.

year period, which indicates ravens have not fully expanded into this MZ.

Human-facilitated expansion of ravens has positioned ravens to become native invaders that can negatively affect populations of sensitive species (Carey et al. 2012). They have become overabundant in many areas within their historic range and have expanded their range into areas that would not have supported their existence or higher abundance prior to human development. Their numbers have increased by >1,000% in the Sonoran Desert and >700% in both the Colorado and West Mojave deserts, USA (Boarman and Kristan 2006, Sauer et al. 2017). Our findings were consistent with other recent studies—either smaller or larger spatial scales—in finding overall increases in raven abundance over time in the western United States and southwestern Canada (Figure 8A; Sauer et al. 2017, Harju et al. 2021). Harju et al. (2021) found 4.6- and 32.4-fold increases in the Cold Deserts and West-Central Semiarid Prairies EPA level II ecoregions from 1966 to 2018, respectively.

In addition, human development throughout the western United States has directly and indirectly subsidized ravens, creating a suite of management challenges for wildlife agencies (Boarman 1993; Coates et al. 2014*a*, *b*; O'Neil et al. 2018; Coates et al. 2020). For example, fledgling success of ravens was higher near roads (Kristan et al. 2004). Roadkill is ephemeral but frequent on highly traveled roads, and anthropogenic structures are abundant on or next to roads. Our evaluation of an inclusive set of predictor variables confirmed our hypothesis that availability of human subsidies (landfills, transmission lines, and overall urbanization) and their increase were mechanisms behind recent increased raven abundance and spatial expansion throughout the range of greater and Gunnison sage-grouse. Urbanization near Fairbanks, Alaska, also resulted in greater numbers of ravens (Baltensperger et al. 2013); Bui et al. (2010) found towns, human development, and landfills were associated with higher raven density in west-central Wyoming (MZ II); and landfills are also known winter subsidy areas for ravens (Baltensperger et al. 2013, Peebles and Conover 2017). Nest success of greater sage-grouse in Nevada, USA (MZ III) was negatively influenced by ravens that were associated with transmission lines (Gibson et al. 2018), and we found a positive relationship between the density of transmission lines and annual intrinsic growth rate in ravens across the range of greater and Gunnison sage-grouse.

We were surprised that cropland, energy development (oil and gas and wind power), and roads were not good predictors of r or K, which was contrary to some of our hypotheses. Coates et al. (2020) found agricultural land and roads were positively connected to raven density, which negatively affected greater sage-grouse nest success; Backensto (2010) found ravens use oil and gas infrastructure in the North Slope of Alaska. Wind power, including ancillary structures, has only been hypothesized or anecdotally observed to contain perch or food subsidies that attract ravens. Our analyses' lack of connecting these anthropogenic subsidies to raven population dynamics may have been a relic of the large spatial extent of our study area, distribution of BBS routes across space, and current population size of ravens throughout MZs. For example, oil and gas development had the most extensive spatial footprint and increase in MZs I and II, which also had the lowest raven abundances across our study, which may indicate ravens have not fully capitalized on human resources associated with oil and gas, as ravens were not more abundant near these resources.

Habitat conversion and fragmentation have benefitted ravens (Andrén 1992, O'Neil et al. 2018, Coates et al. 2020), and wildfire is one of the largest factors fragmenting sagebrush ecosystems (Balch et al. 2013). Wildfire has increased over the past decades throughout the sagebrush ecosystem, especially MZs III, IV, V, and VI, and increased wildfire has been negatively connected to greater sage-grouse population persistence (Coates et al. 2016*b*) and nest success (Foster et al. 2019, O'Neil et al. 2020, Dudley et al. 2021). Interestingly, our results provide evidence for our hypothesis that more ravens were present in sagebrush ecosystem that had burned, and raven carrying capacity was greater in burned areas, indicative of areas providing better habitat for ravens. O'Neil et al. (2020) and Dudley et al. (2021) suggest negative effects of fire on greater sage-grouse nest success and population growth, respectively, were connected to reduced cover, contributing to potential increased predation by ravens. Fire-related increases in raven abundance in sage-grouse habitat and decreased nest success of sage-grouse highlight potentially compounding negative effects of fire to sage-grouse populations. In contrast, we hypothesized that forested areas would provide perches and improved hunting opportunities for ravens, but forested areas were negatively associated with *K* for ravens. This indicates that raven carrying capacity was generally greater in more open environments, especially when there were adequate human resources available. While burned and forested land cover increases may not be directly associated with human endeavors, expansion of trees into sagebrush ecosystems (Miller et al. 2000) and invasive annual grass-fueled fires (Miller et al. 2013) have been related to human management and historic behavior. Fragmentation and edges where intact sagebrush adjoined disturbed areas were associated with high raven occurrence and nest density in Idaho, USA (Coates et al. 2014*a*, *b*; Howe et al. 2014). Habitat fragmentation has detrimental impacts on many species, including greater and Gunnison sage-grouse, and humans continue to expand development more thoroughly into ecosystems.

Ravens continue to benefit from human development and expansion, but their inflated abundance often has detrimental effects on other native species. The sagebrush ecosystem has increased in habitat quality for ravens due to increasing human endeavors. In fact, ravens may actually prefer fragmented habitat and habitat edges in sagebrush ecosystems (Coates et al. 2014*a*, Howe et al. 2014). Greater and Gunnison sage-grouse are sagebrush-obligate species that are extremely sensitive to degradation and disturbance of their habitat (Connelly et al. 2011, Foster et al. 2019). In fragmented landscapes, greater sage-grouse nests may be up to 9 times more likely to be depredated than in intact habitat (Vander Haegen et al. 2002).

Increasing raven populations negatively impact sage-grouse populations (Dinkins et al. 2016, Peebles et al. 2017, Taylor et al. 2017, Gibson et al. 2018, Coates et al. 2020) and space use (Dinkins et al. 2012, 2014), contributing to the long-term decline of greater and possibly Gunnison sage-grouse. Thus, raven populations will require management intervention within some areas shared with sage-grouse to minimize problematic negative effects on sensitive grouse populations. These negatives likely occur for other sensitive species as well (Harju et al. 2021). The area of developed land in the United States increased by 48% from 1982 to 2003 and is predicted to increase 51% between 2003 and 2030 (White et al. 2009), which indicates raven conflicts with sensitive native species are likely to increase.

Management implications

Removal of nesting structure and food subsidies, especially associated with landfills, are imperative to reduce the impacts of ravens on sage-grouse during nesting and brood-rearing. We suggest management agencies also focus on restoration of burned sagebrush that also has human subsidies to minimize compounded negative effects of fire on sage-grouse populations via increased predation by ravens where nesting cover has been lowered. Large-scale monitoring of invasive native predator species, such as ravens, is imperative to predict where management agencies need to be keenly aware of potential impacts and design strategies for mitigation. Data analyzed in our study were obtained from the North American Breeding Bird Survey, a citizen science tool used throughout North America (Ziolkowski et al. 2010, Pardieck et al. 2016), which is a cost-effective method for data collection across large spatial and temporal scales. However, BBS survey route data only provide a very coarse assessment of bird population trends, indicating more intense surveys will be necessary to fully understand the mechanisms driving raven expansion and increase in abundance.

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