

Estimating trends of common raven populations in North America, 1966–2018

SETH M. HARJU, Heron Ecological, LLC., P.O. Box 235, Kingston, ID 83839, USA
seth@heronecological.com

PETER S. COATES, U.S. Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Drive, Suite D, Dixon, CA 95620, USA

SETH J. DETTENMAIER, U.S. Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Drive, Suite D, Dixon, CA 95620, USA

JONATHAN B. DINKINS, Department of Animal and Rangeland Sciences, Oregon State University, 2921 SW Campus Way, Corvallis, OR 97331, USA

PAT J. JACKSON, Nevada Department of Wildlife, 6980 Sierra Parkway, Suite 120, Reno, NV 89511, USA

MICHAEL P. CHENAILLE, U.S. Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Drive, Suite D, Dixon, CA 95620, USA

Abstract: Over the last half century, common raven (*Corvus corax*; raven) populations have increased in abundance across much of North America. Ravens are generalist predators known to depredate the eggs and young of several sensitive species. Quantifying raven population increases at multiple spatial scales across North America will help wildlife resource managers identify areas where population increases present the greatest risk to species conservation. We used a hierarchical Bayesian modeling approach to analyze trends of standardized raven counts from 1966 to 2018 using Breeding Bird Survey data within each Level I and II ecoregion of the United States and Canada. We also compared raven abundance within and outside the distributions of 9 sensitive or endangered species. Although we found substantial evidence that raven populations have increased across North America, populations varied in growth rates and relative abundances among regions. We found 73% of Level I (11/15) and II (25/34) ecoregions demonstrated positive annual population growth rates ranging from 0.2–9.4%. We found higher raven abundance inside versus outside the distributions of 7 of the 9 sensitive species included in our analysis. Gunnison sage-grouse (*Centrocercus minimus*) had the highest discrepancy, with 293% more ravens within compared to outside of their range, followed by greater sandhill crane (*Antigone canadensis tabida*; 280%), and greater sage-grouse (*C. urophasianus*; 204%). Only 2 species, least tern (*Sternula antillarum*) and piping plover (*Charadrius melodus*), indicated lower raven abundance within relative to outside their distributions. Our findings will help wildlife resource managers identify regional trends in abundance of ravens and anticipate which sensitive species are at greatest risk from elevated raven populations. Future research directed at identifying the underlying regional drivers of these trends could help elucidate the most appropriate and responsive management actions and, thereby, guide the development of raven population management plans to mitigate impacts to sensitive species.

Key words: Bayesian modeling, Breeding Bird Survey, *Centrocercus urophasianus*, common raven, *Corvus corax*, ecoregions, greater sage-grouse, management, population trends, subsidized predator

COMMON RAVENS (*Corvus corax*; ravens) have one of the largest distributions of any vertebrate species spanning most of the Holarctic (Boarman and Heinrich 1999). Their worldwide distribution encompasses large portions of Canada, the western United States, parts of northern Europe, Greenland, Iceland, Siberia, south into central China, northern India, and west to northern Africa (Cramp et al. 1994). Key traits of ravens that enable such a wide distribution

include extreme environmental tolerance and high behavioral plasticity. For example, ravens are opportunistic foragers, have an omnivorous diet, and readily exploit novel resources (Boarman and Heinrich 1999). Numerous studies have demonstrated a consistent and robust link between increasing raven populations and anthropogenic resource subsidies from the expanding human presence in the western United States (Kristan and Boarman 2007, Webb et al.

2011). Ravens adapt well to resulting anthropogenic landscape modifications that provide supplemental resources, including food, water, nesting sites, and hunting perches (Knight and Kawashima 1993, Boarman et al. 2006, Kristan and Boarman 2007, Coates et al. 2016). Consequently, in many parts of western North America, raven populations have grown in concert with a persistently expanding human footprint (Leu et al. 2008). In central and eastern North America, ravens appear to be adapting to urban and suburban environments, expanding across large swaths of the continent (Sauer et al. 2017). For example, Dinkins et al. (2021) reported that the proportion of urban landcover within 25 km was positively associated with higher raven carrying capacity in greater sage-grouse (*Centrocercus urophasianus*) and Gunnison sage-grouse (*C. minimus*) habitats.

Increasing numbers of ravens in North America may pose a threat to the maintenance of biodiversity due to their aggressive territorial behavior and proficiency at preying on nests and juveniles of lower trophic level species (Brussee and Coates 2018). Because ravens are effective at exploiting anthropogenic resources, their carrying capacity can become decoupled from the availability of indigenous resources (Boarman 2003). Ravens also continue to prey on other native wildlife species they encounter opportunistically despite the availability of anthropogenic resource subsidies. This creates a state of hyperpredation where ravens can sustain high predation rates on native prey species without being affected by reductions of that prey species (Smith and Quin 1996, Sinclair et al. 1998, Boarman 2003, Kristan and Boarman 2003). Ravens have been documented depredating the nests of greater sandhill cranes (*Antigone canadensis tabida*; Stern et al. 1987; Littlefield 1995, 1999, 2003), greater sage-grouse (Schroeder et al. 1999, Coates et al. 2008, Bell 2011, Hagen 2011), snowy plover (*Charadrius nivosus nivosus*; Ellis et al. 2015, 2020), least tern (*Sternula antillarum*; Avery et al. 1993, Liebezeit and George 2002, Marschalek 2011, Frost 2014), marbled murrelet (*Brachyramphus marmoratus*; Singer et al. 1991, Hamer and Nelson 1995), and San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*; Eggert et al. 2004). Ravens are also known predators of juvenile Mojave desert tortoises (*Gopherus agassizii*; Kristan and Boarman 2003).

The continued expansion of the anthropogenic footprint across western North America (Leu et al. 2008) has likely foreshadowed the increasing negative impacts of ravens on multiple prey species within western ecosystems. However, existing estimates of raven abundance trends are scarce and reported at spatial scales that are often too broad to inform local and regional management plans (Sauer et al. 2017). A more comprehensive understanding of current trends in raven populations will help to identify areas where sensitive prey species may be at an increased risk from raven predation and inform appropriate conservation management strategies.

Our primary objective was to model raven population trends at multiple scales within North America using standardized raven counts from Breeding Bird Survey (BBS; Sauer et al. 2017) data that spans 6 decades. We calculated model estimates for Level I ecoregions, and subsequently, for Level II ecoregions nested within Level I ecoregions. We modeled trends within both levels of ecoregions to provide inference at a variety of ecological and management scales. We also modeled raven abundance at the resolution of within versus outside of 9 individual sensitive species distributions. Our multiscale analysis provides population estimates at multiple resolutions appropriate for informing sensitive species management plans, improving on what has been previously reported.

Study area

The area of analysis in this study is all Level I ($n = 15$) and II ($n = 34$) ecoregions in the continental United States and Canada within which BBS routes were established and surveyed (Figures 1 and 2; Omernik 1987). Ecoregions are major ecological areas where the ecosystem and its component biotic, abiotic, terrestrial, and aquatic components are similar. We modeled raven trends within ecoregions to reflect general associations between raven populations, ecosystems, other sensitive species, and anthropogenic subsidies related to land uses that likely are similar within but vary among ecoregions. Level I ecoregions are broad categorizations, ranging from the Arctic Cordillera in northern Canada, characterized by a harsh climate, rugged terrain, and low biological productivity, to Tropical Wet Forests at the southern tip of the

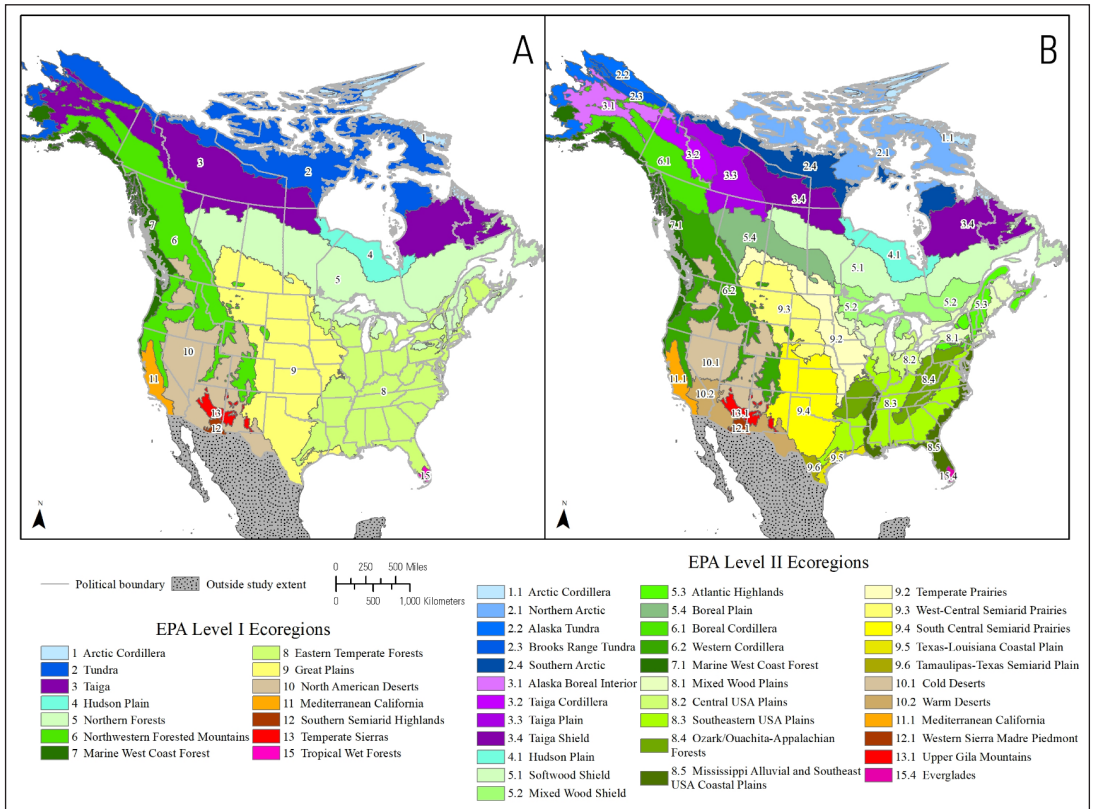


Figure 1. Maps of Level I (A) and Level II (B) ecoregions of the United States and Canada used as strata for modeling common raven (*Corvus corax*) population trends from 1966 to 2018 (Omernik 1987).

Florida Peninsula, USA, characterized by evergreen and semideciduous forests and high biological diversity (Commission for Environmental Cooperation [CEC] 1997; Figure 1). Level II ecoregions are nested within Level I ecoregions and reflect a higher degree of physical, biological, and anthropogenic land use homogeneity. Three Level I ecoregions (Hudson Plain, Marine West Coast Forests, and Mediterranean California) have no subset Level II ecoregions, and thus retain the same boundaries. The CEC (1997) provide a detailed description of ecological regionalization in North America.

Methods

Population trends

To better understand the scope of long-term trends in raven populations, we analyzed standardized raven counts from the BBS data across the continental United States and Canada from 1966 to 2018 (Figure 2; <https://www.pwrc.usgs.gov/bbs/>; Pardieck et al. 2020). A BBS survey involves multiple 3-minute point count surveys

of all avian species, approximately every 0.8 km (0.5 miles) along a 39.4-km (24.5-mile) survey route. At each point count, every bird seen or heard within 0.4 km (0.25 miles) is recorded. As of 2018, there were ~4,100 BBS routes across the continental United States and Canada. The BBS surveys occurred in all Level I and Level II ecoregions of the continental United States and Canada (Figures 1 and 2). We did not analyze BBS routes in Mexico due to their short and recent history and limited spatial coverage.

We modeled trends using the hierarchical Bayesian first-difference model proposed by Link et al. (2017) as a robust improvement over the similar log-linear trend model previously used by the U.S. Geological Survey as described by Sauer and Link (2011). The first-difference model is also more flexible at capturing non-linear population trends and apparent population swings of individual species (Link et al. 2017).

The first-difference model assumed that BBS raven counts follow a Poisson distribution

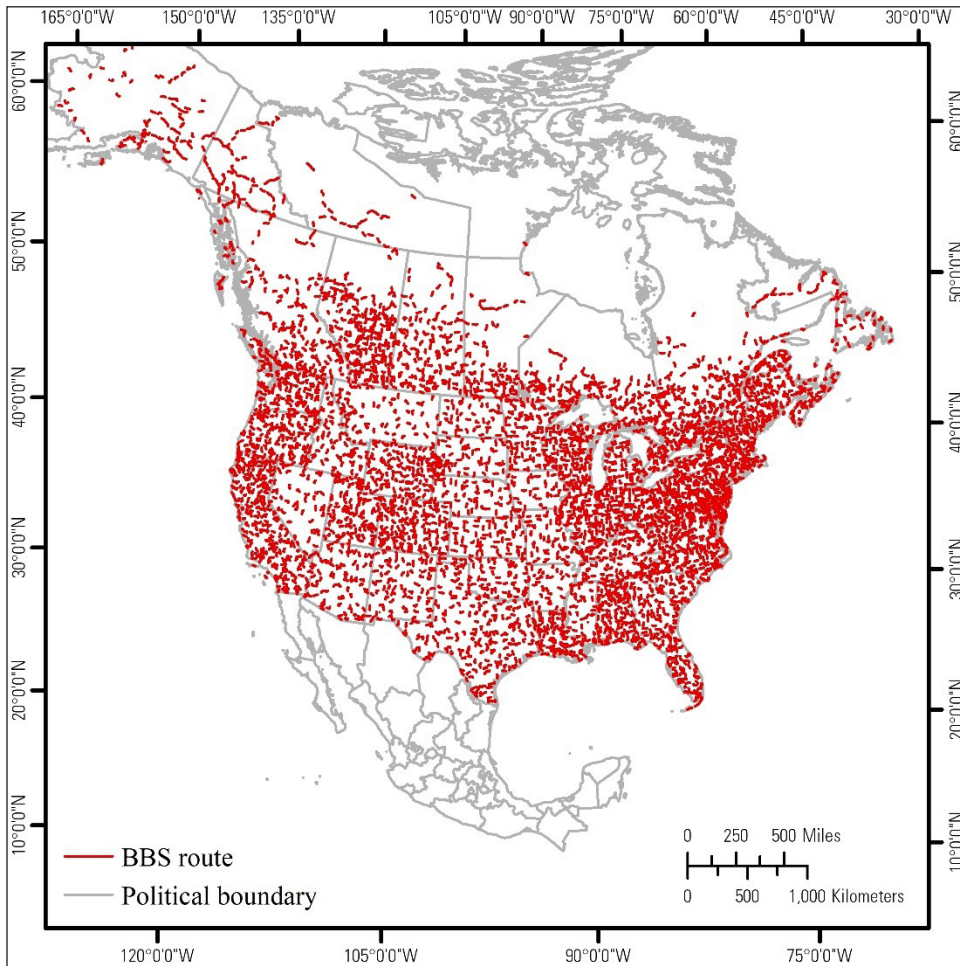


Figure 2. Map of Breeding Bird Survey routes in the continental United States and Canada, surveyed at least once from 1966 to 2018.

specified by a rate parameter ρ (equation 1). Specifically, for the number of ravens C counted on survey k :

$$C_k \sim Pois(\rho_k) \tag{1}$$

The rate parameter ρ_k was a log-linear function of both confounding variables and variables of interest, such that:

$$\log(\rho_k) = \gamma_{st} + \xi_o + \varphi_s + \eta_o + \varepsilon \tag{2}$$

where the log of λ_k was a linear function of a year effect (γ_{st}) for each strata s and year t , a zero-mean random intercept (ξ_o) for each observer o , a zero-mean strata effect (φ_s) for each strata s , a first-year observer startup effect (η_o) whereby inexperienced observers tend to record smaller

counts of individual birds than the same observer in subsequent surveys (Sauer and Link 2011), and a zero-mean overdispersion error term ε . The key component of the first-difference trend model is that each stratum- and year-specific year effect γ_{st} is a Gaussian function of that stratum’s previous year effect:

$$\gamma_{st} \sim Norm(\gamma_{s[t-1]}, \tau_s) \tag{3}$$

where $\gamma_{s[t-1]}$ is the mean value, and τ_s is the stratum-specific precision of the distribution of γ_{st} . In practice, this resulted in shrinkage effects of yearly abundance estimates toward adjacent yearly abundance estimates over time, regularizing trends over long periods while still allowing for annual swings in raven counts (Link et al. 2017). Random effects were modeled with

weakly informative normal priors on real number variables and gamma priors on positive-definite precision parameters.

We used the parameter estimates from the log-linear abundance model to predict model-adjusted raven abundance per BBS route within each stratum. Predicted yearly route-level abundance within each stratum was a function of each year effect (γ), the strata effect (φ), the average observer effect (ξ), and the observed noise (ε) in the count data (equation 4). Mean stratum-specific annual abundances were adjusted by the proportion of BBS routes within the stratum that ever had a raven observation (p). Estimated annual abundance was calculated as:

$$\hat{N}_{st} = \exp(\gamma_{st} + \varphi_s + \bar{\xi} + \varepsilon)p_s \quad (4)$$

We also estimated rates of population change derived from the trend models to quantify growth rates of raven populations over time in 2 ways. First, we calculated the ratio difference of estimated abundance \hat{N} in 2018 versus 1966 within each sample from the posterior distribution (see below), for each ecoregion (equation 5). Although subject to random variation in estimated relative abundance in either given year, this measure reflects an intuitive comparison of abundance “now” versus “then” calculated as:

$$\Delta_s = \frac{\hat{N}_{s2018}}{\hat{N}_{s1966}} \quad (5)$$

Second, we monitored realized annual rates of population change ($\hat{\lambda}$) from one year to the next (equation 6). We note that the first-difference model does not impose a mathematical form on the rate of population change. Thus, our calculation of $\hat{\lambda}$ reflects a data-driven estimate of population change (i.e., derived parameter), conditional on the specification of the first-difference model. It was calculated as:

$$\hat{\lambda}_{st} = \frac{\hat{N}_{s[t+1]}}{\hat{N}_{st}} \quad (6)$$

and was summarized as an annual average rate of population change ($\bar{\lambda}$) across all years within each stratum as:

$$\bar{\lambda}_s = \frac{(\sum_{t=1}^{T-1} \hat{\lambda}_{st})}{(T-1)} \quad (7)$$

We also interpreted population growth rates in percentage terms, calculated as:

$$\% \text{ growth} = (\bar{\lambda}_s - 1) * 100 \quad (8)$$

The first-difference trend model was used to assess raven abundance trends at multiple ecological levels of inference (i.e., strata s in equations 2 and 4). First, we were interested in characterizing raven trends within and among Level I ecoregions. Second, we ran the same models for each Level II ecoregion. We treated ecoregion strata as fully independent from each other (e.g., non-hierarchical).

Sensitive species

In addition to ecoregion strata, we analyzed raven trends specific to 9 species that are “threatened” or “endangered” at the federal, state, or provincial level (Coates et al. 2021c): California condor (*Gymnogyps californianus*), greater sandhill crane, Mojave desert tortoise, greater sage-grouse, Gunnison sage-grouse, marbled murrelet, piping plover (*Charadrius melodus*), snowy plover, and least tern. We chose these species because ravens are known or suspected to be a limiting factor for nest success or survival of these species (Coates et al. 2021c). For each of these analyses, we separated BBS routes into those occurring within each species range, and

Table 1. Numbers of Breeding Bird Surveys conducted in each Level I ecoregion, United States and Canada, 1966–2018.

Level I ecoregions	No. surveys
Arctic Cordillera	2
Eastern Temperate Forests	55,757
Great Plains	21,518
Hudson Plain	36
Marine West Coast Forest	3,154
Mediterranean California	2,576
North American Deserts	10,942
Northern Forests	16,066
Northwestern Forested Mountains	12,032
Southern Semiarid Highlands	283
Taiga	928
Temperate Sierras	643
Tropical Wet Forests	322
Tundra	344
Water	50

Table 2. Median ratio change of modeled common raven (*Corvus corax*) abundance in 2018 compared to 1966 across Level I ecoregions (i.e., the proportional change in abundance over 53 years). Two ecoregions had no observed ravens on any survey routes (na; Arctic Cordillera and Tropical Wet Forests) Ecoregions with an asterisk (*) had 95% CrI that did not overlap 1.0. L. and U. 95% CrI are lower and upper 95% Bayesian credible intervals, respectively. For example, in Eastern Temperate Forests, raven abundance was 3.9 times higher (95% CrI 3.2–4.9) in 2018 than in 1966.

Ecoregion	Ratio change	L. 95% CrI	U. 95% CrI
Arctic Cordillera	na	na	na
Eastern Temperate Forests*	3.9	3.2	4.9
Great Plains*	23.4	16.8	32.1
Hudson Plain	0.8	0.3	2.3
Marine West Coast Forest*	3.1	2.0	5.1
Mediterranean California*	14.3	7.7	26.4
North American Deserts*	6.2	4.2	9.3
Northern Forests*	4.6	3.4	6.0
Northwestern Forested Mountains*	6.0	4.0	8.8
Southern Semiarid Highlands	1.9	0.7	5.0
Taiga	1.0	0.4	2.3
Temperate Sierras*	3.5	1.7	7.6
Tropical Wet Forests	na	na	na
Tundra	0.8	0.3	2.0
Water	1.1	0.3	3.4

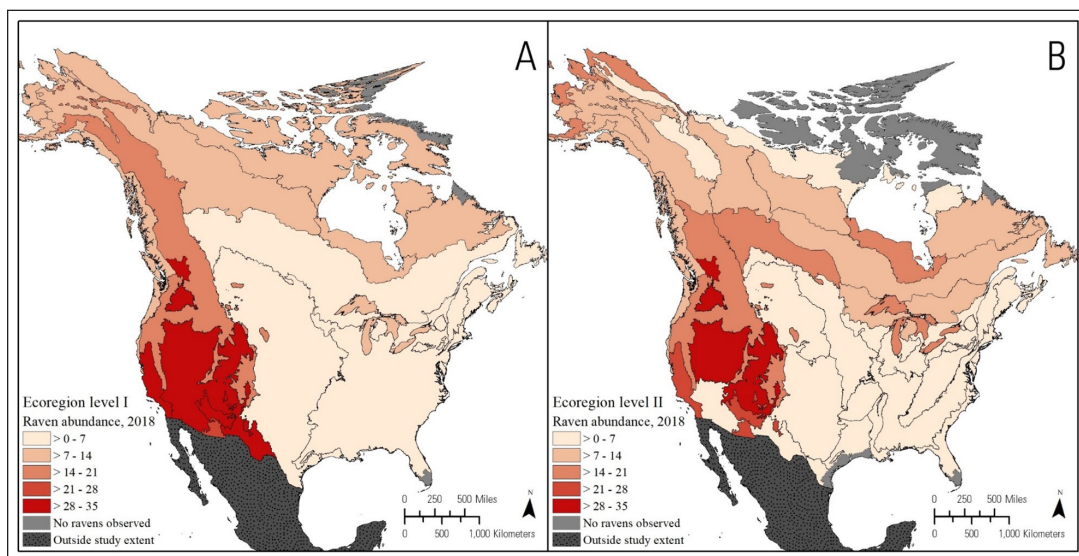


Figure 3. Maps of estimated relative common raven (*Corvus corax*) abundance (number of ravens / Breeding Bird Survey route) in 2018 within Level I (A) and Level II (B) ecoregions, United States and Canada.

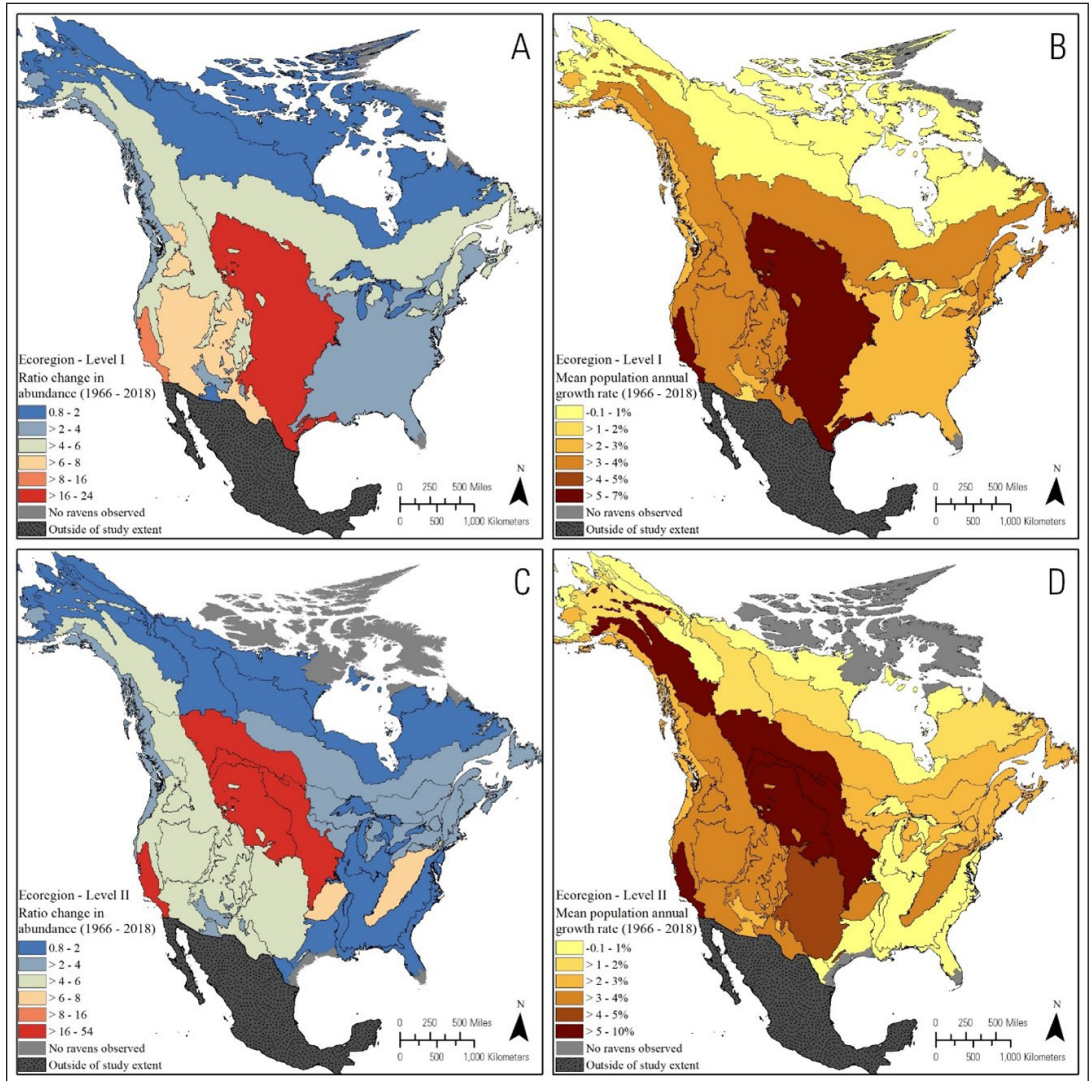


Figure 4. Maps of common raven (*Corvus corax*) abundance trends within Level I (A and B) and Level II (C and D) ecoregions of the United States and Canada, 1966–2018. Panels A and C are the ratio difference in estimated abundance in 2018 vs. 1966 for each ecoregion (i.e., $2018_N / 1966_N$). Panels B and D are mean estimated annual population growth rate within each ecoregion, 1966–2018.

those outside of each species range. Species' ranges included all seasonal ranges for both migratory and non-migratory species (BirdLife International 2019). The model structure was the same as that for the ecoregion trend analyses, except instead of strata being ecoregions, there were 2 strata for each species model: within and outside of the sensitive species' range.

All models were fit using Markov Chain Monte Carlo (MCMC) methods in JAGS (v4.2.0; <http://mcmc-jags.sourceforge.net/>) via the "R2jags" interface in Program R (v3.6.3). Mod-

els were run on 3 chains, thinning by 2 iterations, for 11,000 iterations with a burn-in period of 2,000 iterations, yielding 13,500 draws from the joint posterior distribution. Unless otherwise specified, mean posterior parameter estimates are presented with 95% Bayesian credible intervals (CrI). Convergence was assessed via monitoring trace plots of posterior draws of monitored nodes and via the R-hat diagnostic, assuming that nodes with R-hat values <1.10 represented successful convergence on the posterior distribution (Gelman and Rubin 1992).

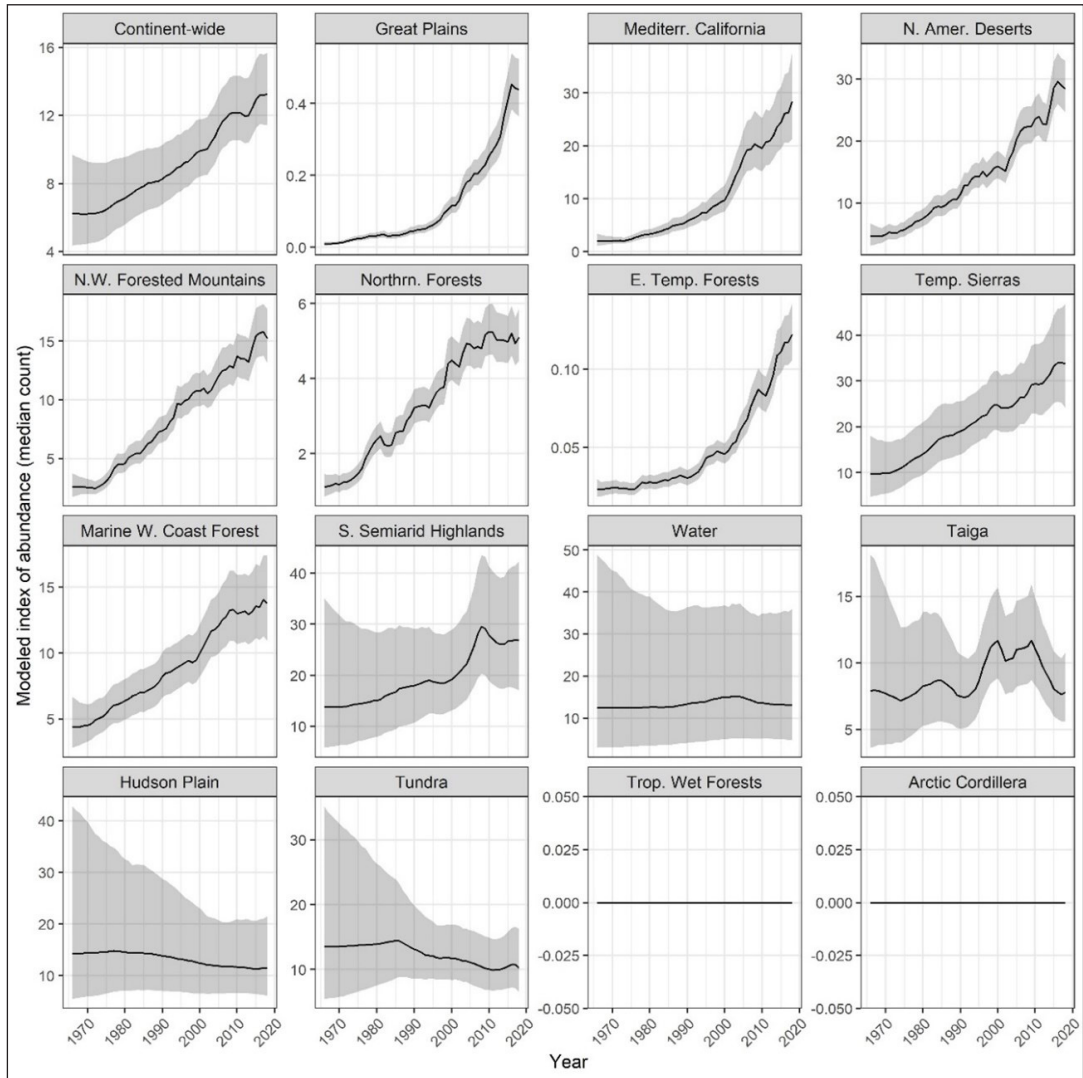


Figure 5. Common raven (ravens; *Corvus corax*) abundance trends within Level I ecoregions (number of ravens per Breeding Bird Survey [BBS] route survey), including continent-wide average abundance trend, with 95% credible intervals. Note variable y-axis scales. Tropical Wet Forests and Arctic Cordillera had zero ravens ever observed on a BBS route.

Results

Population trends

The MCMC chains for most nodes met successful convergence criteria. We found 93.3% of nodes had R-hat values <1.10 (highest R-hat = 1.16) for Level I ecoregion year-specific abundance estimates. For Level II ecoregions, 92.3% of year- and ecoregion-specific abundance nodes had R-hat values <1.10 . R-hats >1.10 (highest R-hat = 1.34) were always associated with nodes from ecoregions with few surveys conducted over the 53-year modeling period.

Level I ecoregions. Survey effort (i.e., number

of BBS routes surveyed) varied markedly across Level I ecoregions, ranging from 2 to $>55,000$ surveys (Table 1). Ravens were observed in all Level I ecoregions except for Arctic Cordillera and Tropical Wet Forests, the most northern and southern Level I ecoregions, respectively, in Canada and the United States. Eight of 15 Level I ecoregions showed substantial evidence of population increases in raven abundance, ranging from 3.1–23.4 times higher abundances in 2018 compared to 1966 (Table 2: Coates et al. (2021a)). We found raven abundance in the Great Plains, Mediterranean California, and

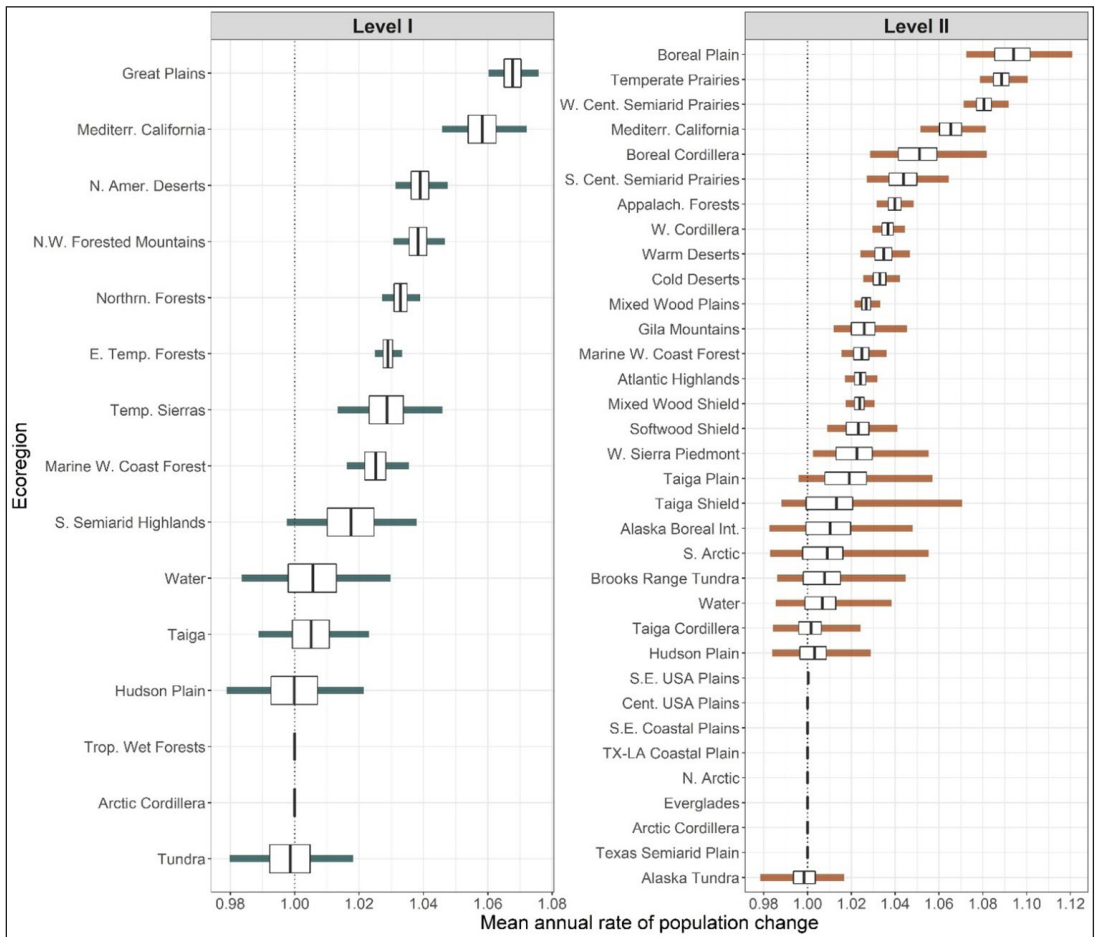


Figure 6. Mean annual rate of common raven (raven; *Corvus corax*) population growth (λ) in Level I and Level II ecoregions, United States and Canada, 1966–2018. A value of 1.0 (vertical dotted line) represents constant abundance from year to year. Vertical black bars are mean growth rate, white boxes are 50% Bayesian credible intervals, and horizontal colored bars are 95% credible intervals. For example, raven populations in the Northwestern Forested Mountains ecoregion increased by a factor of 1.038 (95% CrI 1.031–1.047) every year, on average, from 1966 to 2018.

North American Deserts was 23.4 (95% CrI = 16.8–32.1), 14.3 (95% CrI = 7.7–26.4), and 6.2 (95% CrI = 4.2–9.3) times greater in 2018 than in 1966, respectively.

Spatially, in 2018 raven abundance was highest in western and north-central North America and lowest in central and southeastern ecoregions (Figure 3A). In slight contrast, the highest rates of growth in raven abundance, both in the ratio change in abundance and annual $\hat{\lambda}$, were in central North America and far southwestern United States. (i.e., Mediterranean California; Figures 4A and 4B).

Although our models indicated substantial variation in raven population abundance and trends across Level I ecoregions, overall abun-

dance has substantially increased continent-wide from 1966 to 2018 (Figure 5). Ecoregions with the greatest relative abundance during 2018 and evidence of greatest increasing trends were Mediterranean California, North American Deserts, Southern Semiarid Highlands, and Temperate Sierras, which were located in the most southwestern areas with xeric conditions. However, precision of estimation was generally low for Southern Semiarid Highlands and Temperate Sierras, which was likely attributable to their small geographic extents and limited amount of survey data (Table 1).

For the medium abundance estimates of 2018, we found no discernable trends in the far northern ecoregions of Hudson Plain, Taiga, Tundra,

Table 3. Numbers of Breeding Bird Surveys conducted in each Level II ecoregion, United States and Canada, 1966–2018.

Level II ecoregions	No. surveys	Level II ecoregions	No. surveys
Alaska Boreal Interior	522	Ozark/Ouachita-Appalachian Forests	11,291
Alaska Tundra	262	Softwood Shield	1,376
Arctic Cordillera	2	South Central Semiarid Prairies	7,595
Atlantic Highlands	6,401	Southeastern USA Plains	17,985
Boreal Cordillera	972	Southern Arctic	27
Boreal Plain	1,965	Taiga Cordillera	109
Brooks Range Tundra	53	Taiga Plain	178
Central USA Plains	4,802	Taiga Shield	119
Cold Deserts	8,563	Tamaulipas-Texas Semiarid Plain	174
Everglades	322	Temperate Prairies	7,184
Hudson Plain	36	Texas-Louisiana Coastal Plain	1,122
Marine West Coast Forest	3,154	Upper Gila Mountains	643
Mediterranean California	2,576	Warm Deserts	2,379
Mississippi Alluvial and Southeast USA Coastal Plains	7,807	Water	50
Mixed Wood Plains	13,872	West-Central Semiarid Prairies	5,443
Mixed Wood Shield	6,324	Western Cordillera	11,060

and Water (Table 1; Figure 5), yet we found steady increases through time in northwestern areas of Marine West Coast Forest, Northwestern Forested Mountains, and Northern Forests (Figure 5). Despite low relative abundance, we also found that populations increased over the past 3 decades in Eastern Temperate Forest and exponentially increased in terms of relative abundance over the past 2 decades in Great Plains (Figure 5).

Estimated continent-wide annual $\hat{\lambda}$ was, on average, 1.015 (CrI = 1.006–1.022), every year for 53 years. We also found variation in annual $\hat{\lambda}$ across ecoregions. For example, 11 of the 15 Level I ecoregions had estimated positive annual $\hat{\lambda}$, and 8 of these had $\hat{\lambda}$ whose credible intervals did not overlap 1.0, ranging from 2.5–6.8% growth every year, on average, from 1966 to 2018 (Figure 6). The highest annual $\hat{\lambda}$ were estimated in Great Plains (6.8%, CrI = 6.0–7.6%), Mediterranean California (5.8%, CrI = 4.6–7.2%), and North American Deserts (3.9%, CrI = 3.1–4.8%). Two ecoregions recorded no ravens (Arctic Cordillera and Tropical Wet Forest), and 2 ecoregions (Hudson Plain and Tundra) had weak evidence of a de-

cline in abundance (Table 2).

Level II ecoregions. Survey effort also varied markedly across Level II ecoregions, ranging from 2 to >17,000 surveys (Table 3). Of the 34 Level II ecoregions in the United States and Canada, only 4 did not have ravens observed on BBS routes: Arctic Cordillera, Everglades, Northern Arctic, and Texas-Louisiana Coastal Plain. Eighteen of the 34 ecoregions had substantial evidence of increases in raven abundance, particularly in the Boreal Plain, Temperate Prairies, and West Central Semiarid Prairies, with 53.6 times (CrI = 21.8–76.0), 48.4 times (CrI = 34.2–67.1), and 32.4 times (CrI = 22.6–44.8) as many ravens in 2018 as 1966, respectively (Table 4).

Level II ecoregion spatial patterns in population growth were similar to those of Level I, with the highest ratio change in abundance in central North America and the far southwest and the highest annual growth rates in central North America, the far southwest, and northwestern Canada and portions of Alaska (Figures 4C and 4D). Also notable at the finer scale of Level II ecoregions was the higher-than-regional population growth in the Appalachian

Table 4. Median ratio change of modeled common raven (*Corvus corax*) abundance in 2018 compared to 1966 across Level II ecoregions. Four ecoregions had no observed ravens on any survey routes (represented by na). Ecoregions with an asterisk (*) had 95% CrI that did not overlap 1.0. L. and U. 95% CrI are lower and upper 95% Bayesian credible intervals, respectively. For example, in Cold Deserts, raven abundance was 4.6 times higher (95% CrI 3.2–6.9) in 2018 than in 1966.

Ecoregion	Ratio change	L. 95% CrI	U. 95% CrI
Alaska Boreal Interior	0.8	0.2	3.1
Alaska Tundra	0.8	0.2	1.8
Arctic Cordillera	na	na	na
Atlantic Highlands*	3.0	2.1	4.1
Boreal Cordillera*	6.0	2.1	20.4
Boreal Plain*	53.6	21.8	76.0
Brooks Range Tundra	1.1	0.4	5.2
Central USA Plains*	1.0	1.0	1.0
Cold Deserts*	4.6	3.2	6.9
Everglades	na	na	na
Hudson Plain	0.9	0.3	2.8
Marine West Coast Forest*	3.1	2.1	5.2
Mediterranean California*	18.1	9.4	35.1
Mississippi Alluvial and Southeast USA Coastal Plains	1.0	1.0	1.0
Mixed Wood Plains*	3.4	2.6	4.5
Mixed Wood Shield*	2.9	2.1	4.1
Northern Arctic	na	na	na
Ozark/Ouachita-Appalachian Forests*	6.1	4.1	8.8
Softwood Shield*	2.4	1.3	5.0
South Central Semiarid Prairies*	5.7	3.0	11.4
Southeastern USA Plains*	1.0	1.0	1.0
Southern Arctic	1.1	0.3	7.3
Taiga Cordillera	0.9	0.3	2.4
Taiga Plain	1.7	0.6	6.3
Taiga Shield	1.2	0.4	8.7
Tamaulipas-Texas Semiarid Plain	1.0	1.0	1.0
Temperate Prairies*	48.4	34.2	67.1
Texas-Louisiana Coastal Plain	na	na	na
Upper Gila Mountains*	3.0	1.6	6.9
Warm Deserts*	4.7	2.8	8.0
Water	1.1	0.3	3.5
West-Central Semiarid Prairies*	32.4	22.6	44.8
Western Cordillera*	5.5	3.8	8.0
Western Sierra Madre Piedmont	2.1	0.9	7.6

Forests. Combined with Figure 3B, it was clear that although total 2018 raven abundances remain low in the central and Appalachian Forests region, they have experienced high rates of growth over the past 53 years.

Of the 16 ecoregions with minimal evidence of trends (including the 4 ecoregions with zero raven observations), 14 had <525 BBS surveys over the 53 years, limiting our statistical ability to make confident estimations of temporal trends. The exceptions were 2 ecoregions with a high number of surveys, Mississippi Alluvial and Southeast USA Coastal Plains (n surveys = 7,807) and Texas-Louisiana Coastal Plain (n = 1,122), suggesting confidence in the assessment of no statistical trend in abundance (Southeast USA Coastal Plains) or raven absence (Texas-Louisiana Coastal Plain). One ecoregion (Upper Gila Mountains, n = 643) had a low number of surveys but showed strong evidence of higher raven abundance in 2018 than 1966. All other ecoregions with evidence of increasing trends had between 972 and 17,985 BBS surveys.

For Level II ecoregions, 20 of the 34 ecoregions had clear or likely increases in raven abundance over time (Figure 7). The remaining 14 ecoregions had inconclusive trends (n = 10) or had zero raven observations (n = 4; supplemental material). The shape of increasing trends in abundance ranged from linear to exponential over time and did so regardless of initial raven abundance, which varied considerably (Figure 7; note variable y-axes).

Nineteen of the 34 ecoregions had annual $\hat{\lambda}$ whose credible intervals did not overlap 1.0, indicating statistically significant positive population growth. Seventeen of the 19 had average estimated annual growth rates >2.0% every year for 53 years (Figure 6). The 5 ecoregions with the highest annual growth rates were Boreal Plain (9.4 %, CrI 7.2–12.1%), Temperate Prairies (8.9%, CrI 7.9–10.1%), West Central Semiarid Prairies (8.1%, CrI 7.1–9.2%), Mediterranean California (6.5%, CrI 5.2–8.1%), and Boreal Cordillera (5.1%, CrI 2.9–8.2%).

Sensitive species

The proportion of BBS routes that fell within the distributions of listed species we investigated varied from 0.7–64.7% (Table 5). For 7 of the 9 species we assessed, raven populations were higher and had increased more inside than out-

side the range of those species, including greater sandhill crane, greater sage-grouse, California condor, Gunnison sage-grouse, Mojave desert tortoise, marbled murrelet, and snowy plover (Figure 8). The higher density of ravens in these species' range may portend the disproportionate risk that ravens pose relative to the general increase in raven populations across the continent. For 2 species, piping plover and least tern, raven populations were small and exhibited minimal growth over time even as they rose dramatically outside of these 2 species ranges (Table 6; Figure 8). This suggests that for these 2 species, the potential risk from ravens has remained constant over time, regardless of continent-wide raven population increases.

Discussion

Our study is the first comprehensive trend analysis of raven population abundances across ecoregions, which may be the scale most relevant to resource management agencies. Previous trend estimates have been limited either to the continental-scale (Sauer et al. 2017) or relatively small local geographic extents (Dinkins et al. 2016, Conover and Roberts 2017); however, see also Dinkins et al. (2021) for a raven analysis across both greater and Gunnison sage-grouse distributions. We have provided clear and predictable patterns of increases in raven abundance across the continent over the past 5 decades, which corroborates the continent-wide estimate of annual population growth of 2.87% reported previously (Sauer et al. 2017). However, our results demonstrated substantial variation in raven population growth rates between ecoregions, especially at Level II. For example, mean annual $\hat{\lambda}$ was highest in the Boreal Plain (9.4% or $\hat{\lambda}$ = 1.094) and lowest in Tundra (-0.1% or $\hat{\lambda}$ = 0.999). Additionally, our analysis is the first to evaluate trends of ravens within the distributional boundaries of sensitive prey species, which could help inform threats of elevated predation risk (Boarman 2003, Kristan and Boarman 2003).

Of the 34 Level II ecoregions, the 3 with the highest estimated abundance in 2018 were in western North America: the Cold Deserts, Upper Gila Mountains, and Mediterranean California. These total abundance estimates and the trends leading up to them could be concerning to western resource managers where ravens are

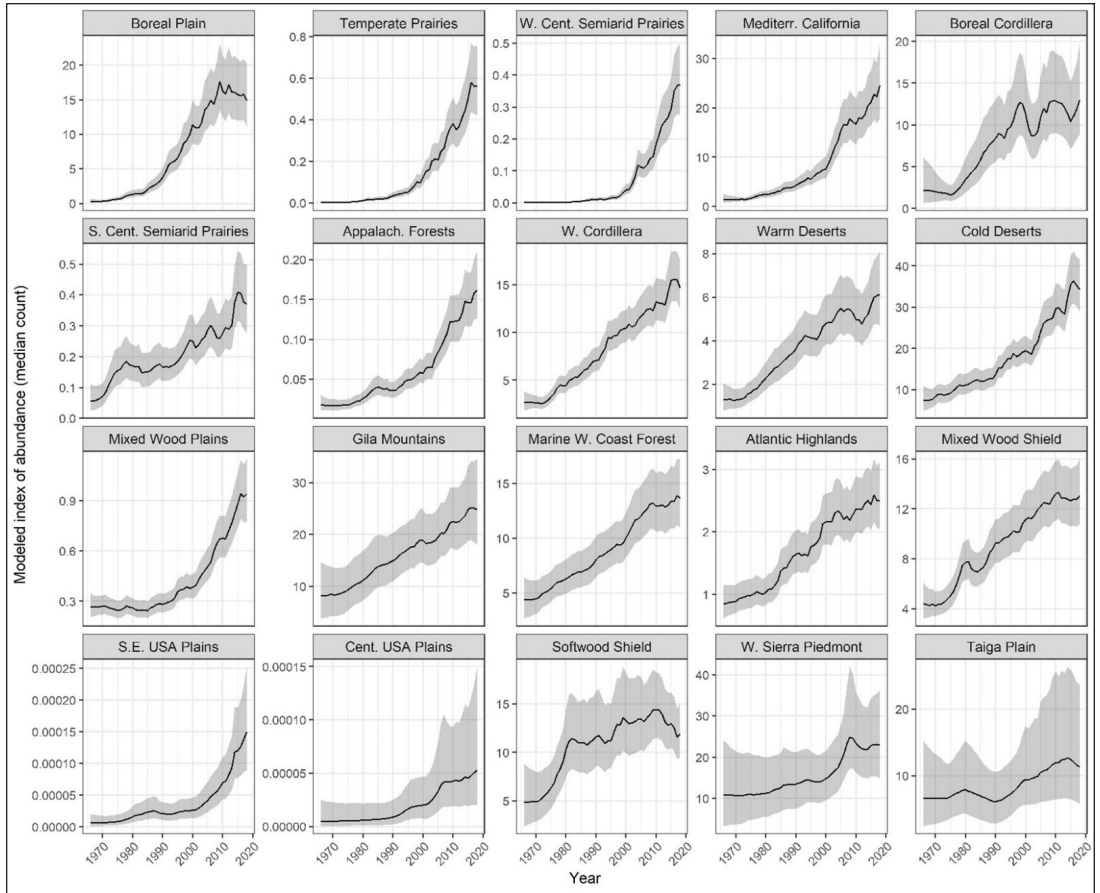


Figure 7. Common raven (ravens; *Corvus corax*) abundance trends within Level II ecoregions (number of ravens per Breeding Bird Survey route), with 95% credible intervals. Note variable y-axis scales. Of the 34 Level II ecoregions in the United States and Canada, only the 20 ecoregions with strongest trends are presented here. See supplemental material for estimated trends in the remaining 14 ecoregions.

Table 5. Percent of all Breeding Bird Surveys (BBS) conducted within federally or state/province listed “threatened” or “endangered” species’ annual ranges, United States and Canada, 1966–2018.

Species	Percent BBS surveys within range
California condor (<i>Gymnogyps californianus</i>)	5.9
Mojave desert tortoise (<i>Gopherus agassizii</i>)	1.8
Greater sage-grouse (<i>Centrocercus urophasianus</i>)	9.3
Gunnison sage-grouse (<i>Centrocercus minimus</i>)	0.7
Marbled murrelet (<i>Brachyramphus marmoratus</i>)	2.8
Greater sandhill crane (<i>Antigone canadensis tabida</i>)	64.7
Snowy plover (<i>Charadrius nivosus nivosus</i>)	11.4
Least tern (<i>Sternula antillarum</i>)	12.0
Piping plover (<i>Charadrius melodus</i>)	62.2

Table 6. Modeled common raven (*Corvus corax*) abundance (number per Breeding Bird Survey route survey) within and outside of federally or state/province listed “threatened” or “endangered” species’ annual ranges in 2018. Percent increase calculated as $(N_{\text{within}} / N_{\text{outside}}) - 100$.

Species	Species’ range	Abundance	L. 95% CrI	U. 95% CrI	% Increase
California condor (<i>Gymnogyps californianus</i>)	Within range	8.21	6.66	10.10	179.5
	Outside range	2.94	2.66	3.30	
Mojave desert tortoise (<i>Gopherus agassizii</i>)	Within range	6.72	4.97	9.44	110.4
	Outside range	3.19	2.87	3.62	
Greater sage-grouse (<i>Centrocercus urophasianus</i>)	Within range	8.33	7.03	9.93	203.9
	Outside range	2.74	2.47	3.09	
Gunnison sage-grouse (<i>Centrocercus minimus</i>)	Within range	10.56	7.90	14.08	293.4
	Outside range	2.68	2.47	2.93	
Marbled murrelet (<i>Brachyramphus marmoratus</i>)	Within range	6.04	4.68	7.81	92.0
	Outside range	3.15	2.85	3.54	
Greater sandhill crane (<i>Antigone canadensis tabida</i>)	Within range	3.97	3.60	4.40	280.6
	Outside range	1.04	0.92	1.20	
Snowy plover (<i>Charadrius nivosus nivosus</i>)	Within range	5.19	4.30	6.27	76.3
	Outside range	2.94	2.66	3.32	
Least tern (<i>Sternula antillarum</i>)	Within range	0.03	0.02	0.04	-99.3
	Outside range	3.86	3.48	4.56	
Piping plover (<i>Charadrius melodus</i>)	Within range	0.31	0.26	0.37	-96.8
	Outside range	9.61	8.53	10.96	

reported to depredate the nests and juveniles of state and federally listed species, such as greater sandhill cranes (Stern et al. 1987; Littlefield 1995, 1999, 2003), snowy plovers (Lauten et al. 2006; Ellis et al. 2015, 2020), least terns (Liebezeit and George 2002, Marschalek 2011), marbled murrelets (Manly et al. 1999), California condors (Mee and Snyder 2007), greater sage-grouse (Coates et al. 2008, Lockyer et al. 2013, Coates et al. 2020), San Clemente loggerhead shrikes (Eggert et al. 2004, Cooper et al. 2005), and Mojave desert tortoises (Kristan and Boarman 2003). For example, the Cold Desert ecoregion is mostly comprised of the Great Basin Desert, which is characterized primarily by sagebrush (*Artemisia* spp.) ecosystems with integrated agricultural activities and exurban development. Recent studies in these ecosystems indicate that raven occupancy and density increases with agricultural activities and anthropogenic structures such as powerlines (O’Neil et al. 2018, Coates et al. 2020). Increases in raven density at broad-scales is associated with reduced greater sage-grouse nest survival,

which was reported to have substantial impacts across ~ 64% of greater sage-grouse breeding areas (Coates et al. 2020). Further investigations may be needed for these species and others to determine whether elevated raven populations contribute to population decline through reduced reproductive productivity.

Regionally, large-scale changes in land use may be driving positive trends in raven abundance. For example, the Boreal Plain had both the highest average annual rate of raven population growth and the largest total magnitude of change among Level II ecoregions (Figure 4; Table 4). Temporally, this coincided with a boom in oil and oil sand production in the Boreal Plain beginning in 1967 that continues to the present day (Alberta Energy 2016, Parson and Ray 2016). Anthropogenic subsidies associated with energy development (e.g., food, nesting substrates, mesopredator release, etc.) may underlie the rapid increase in raven abundance within this region. Alternatively, factors driving dramatic increases in the rate of population growth in an ecoregion may have spillover and

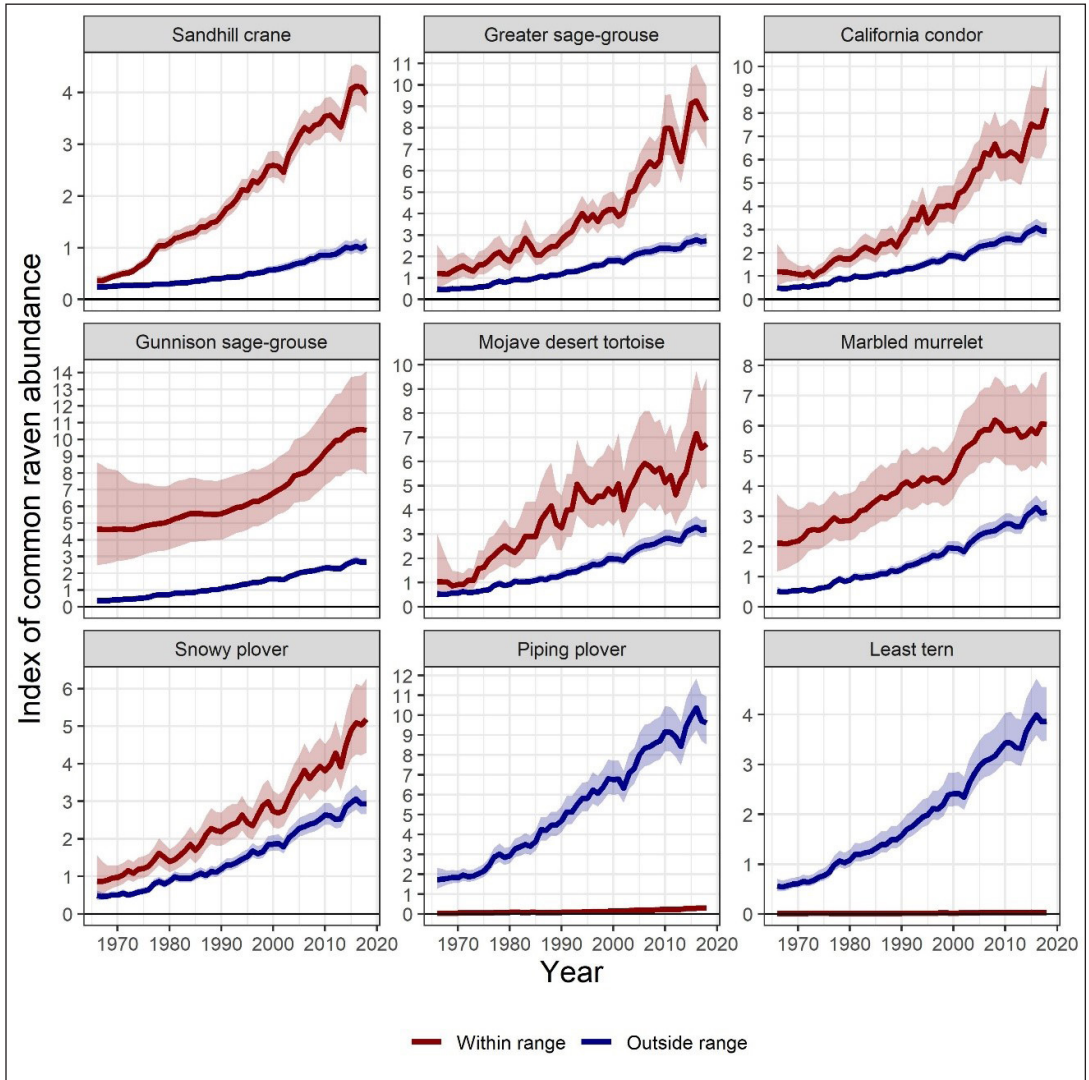


Figure 8. Common raven (ravens; *Corvus corax*) abundance trends within and outside of the year-round ranges of 9 species (sandhill crane, *Antigone canadensis tabida*; greater sage-grouse, *Centrocercus urophasianus*; California condor, *Gymnogyps californianus*; Gunnison sage-grouse, *Centrocercus minimus*; Mojave desert tortoise, *Gopherus agassizii*; marbled murrelet, *Brachyramphus marmoratus*; snowy plover, *Charadrius nivosus*; piping plover, *Charadrius melodus*; and least tern, *Sterna antillarum*) for which ravens are known or potential nest and/or juvenile predators, with 95% credible intervals. Note variable y-axes among species.

expansion effects in neighboring ecoregions (Fox et al. 2005). For example, Mediterranean California showed a rapid increase in growth rate beginning in 2000, and the neighboring Warm Deserts and Cold Deserts ecoregions showed increases delayed by approximately 2 years, possibly reflecting dispersal from high abundance to lower abundance populations (Fleischer et al. 2008; Figure 7).

Differential abundances and population growth rates within and among ecoregions are

likely driven by multiple local mechanisms. As synanthropic omnivores (Boarman and Heinrich 1999), raven populations are known to benefit from an association with anthropogenic subsidies and have been identified as indicators of human disturbance and development (Boarman 2003, Kristan and Boarman 2003, Coates et al. 2014a, Howe et al. 2014, O’Neil et al. 2018). Increased raven occurrence is also associated with agriculture (Engel and Young 1992, Knight et al. 1993, Kelly et al. 2002, Webb et al. 2009).

Coates et al. (2014b) found raven densities were higher in areas associated with livestock production, with the odds of raven occurrence documented to be >45% in areas where livestock was present (Coates et al. 2016). Raven reproduction and survival are also elevated in relation to their proximity to and use of human settlements (Webb et al. 2004, Marzluff and Natherlin 2006, Webb et al. 2011) with higher densities at lower relative elevations comprising increased agriculture and development (Coates et al. 2020). Several studies have determined that nest proximity to point resource subsidies relates to increased nest productivity (Kristan and Boarman 2007) and juvenile survival (Webb et al. 2004). Additionally, the use of point subsidies by ravens is associated with increased survival (Webb et al. 2011, Peebles and Conover 2017). In arid ecoregions like those identified in our models as having the highest rates of increase, raven occurrence and resource use increased in association with supplemental water (Knight et al. 1998, Boarman and Coe 2002, Hanks et al. 2009, Coates et al. 2016).

Other anthropogenic subsidies may also drive observed increases in raven abundance. Ravens also take advantage of human-made infrastructure as roosting (Engel et al. 1992) or nesting substrates (White and Tanner-White 1988, Knight and Kawashima 1993, Steenhof et al. 1993, Kristan and Boarman 2007, Bui et al. 2010, Coates et al. 2014b, Howe et al. 2014). Coates et al. (2014a) found that the probability of raven occurrence was approximately 25% greater within 2.2 km of transmission lines. Another study by Howe et al. (2014) found that ravens in eastern Idaho, USA readily used anthropogenic structures for nesting, with 58% of the 82 nests located on transmission poles and an additional 14% on other human-made towers; power poles and other towers provide elevated perching and nesting locations in areas where these features were historically nonexistent or uncommon. Raven occupancy increases in the Great Basin region when transmission lines co-occur with other anthropogenic indicators, such as increased road densities (O'Neil et al. 2018). In a portion of Wyoming, USA, >95% of raven nests were on human-built infrastructure, particularly that associated with oil and gas development (Harju et al. 2018).

Our models demonstrated larger increases in

raven abundance inside versus outside of the distribution of 7 of the 9 listed species that we assessed. Potential impacts of raven population increases on these 7 species may thus be disproportionately higher than increased raven impacts continent-wide, with implications for species conservation. For example, disproportionately elevated rangewide risk of raven depredation can be linked to vital rates of declining prey populations. Ecoregion-wide increases in raven abundance in Cold Deserts has coincided with rangewide declines in greater sage-grouse abundance (Coates et al. 2021b). At intermediate scales (e.g., landscape level), raven abundance has been experimentally demonstrated to be negatively associated with greater sage-grouse abundance (Peebles et al. 2017). The individual mechanisms behind these patterns are well documented: nest success is a primary driver of greater sage-grouse population growth (Taylor et al. 2012), nest failure is overwhelmingly caused by depredation (Moynahan et al. 2007, Lockyer et al. 2013), and ravens can be the major predator of greater sage-grouse nests (Coates et al. 2008, Lockyer et al. 2013, Taylor et al. 2017).

Estimates of a strongly increasing trend in raven abundance were not always indicative of high numbers of ravens in those ecoregions. Instead, these were frequently the result of relatively small increases in numbers of ravens observed over the 50 years of surveys for ecoregions with relatively low or nonexistent initial raven observations (i.e., potential areas of raven range expansion). For example, the estimated ratio change in raven abundance for the Level II Temperate Prairies ecoregion was 48.4. However, the modeled index of abundance for this ecoregion never exceeded 0.6 ravens/BBS survey. The large rate of change was driven by the absence of observed ravens in the initial survey years. In contrast, the ratio change in Alaska Tundra was only 0.8 despite a mean index of abundance near 20, which is >30 times more ravens than those observed within the Temperate Prairies. Another important contrast is Cold Deserts (Level II), where the ratio difference in 2018 compared to 2016 was a moderate 4.6, but only because of higher initial raven abundances. The total number of ravens per Cold Deserts BBS route increased from ~7 in 1966 to ~35 in 2018, with concomitant increases in relative predation risk for prey populations (Figure 5).

We chose to analyze raven trends at both Level I and II ecoregions, which entails a high level of redundancy, as Level II ecoregions are nested within Level I ecoregions. We did this to provide 2 scales of inference: Level I ecoregions reflect broad processes across large portions of North America and Level II ecoregions reflect more regional trends in raven abundance. As guidance for readers, we suggest that using these results for on-the-ground management purposes (e.g., lethal raven removal or anthropogenic subsidy reduction) would best be done using the Level II results.

The BBS surveys are conducted along developed roadways, and it is possible that ravens occur at higher abundances along roadways, thus potentially biasing survey results (but see Bui et al. 2010). Equally, apparent increases in raven abundance along roadways may not reflect changes in raven abundance in more remote portions of the landscape. Nonetheless, by virtue of its standardization, the BBS data should allow for meaningful comparison of relative trends within and among ecoregions.

We found that sample size was strongly related to our ability to detect meaningful trends. For the 7 non-meaningful Level I ecoregions, the lack of apparent trend may be the product of low sample sizes, as all of these ecoregions had <950 total BBS surveys conducted over 53 years (Table 1). In contrast, the remaining 8 Level I ecoregions all exhibited strong increases in abundance and also had >2,500 BBS surveys over the same period. We cannot conclude that raven populations were stable in the 7 former ecoregions, only that we detected neither the presence nor absence of a trend in ecoregions where few surveys were conducted. In other words, out of 49 ecoregions assessed, ecoregions with $\geq 1,000$ BBS surveys showed strong increases in abundance (with 1 exception), and ecoregions with $\leq 1,000$ BBS surveys were inconclusive (with 1 exception).

Management implications

Our findings suggest that over the past 53 years, raven distributions have expanded across North America and their populations have increased throughout the western and central United States and Canada, while their distributions have expanded across North America. Whether historically common, rare, or absent,

raven abundance has increased several fold over historic abundances. Previous research implicates anthropogenic development as one of the main drivers of these trends. Additional modeling that incorporates raven biology factors into abundance trend modeling could better support our understanding of the underlying mechanisms. Conducting these analyses at similar spatial scales could help inform future conservation management plans by identifying the specific factors influencing these trends in areas where ravens and sensitive species distributions overlap.

Supplemental material

Supplemental material can be viewed at <https://digitalcommons.usu.edu/hwi/vol15/iss3/5>.

Acknowledgments

The authors would like to thank S. Espinosa and the Nevada Department of Wildlife for financial and logistical support of this effort. Thanks to F. McDuire and S. O'Neil for constructive feedback and comments that improved the manuscript. We thank the editors of *Human–Wildlife Interactions*, including T. Messmer, and anonymous reviewers whose comments enriched and added clarity to the manuscript. Additional funding support was provided by the U.S. Geological Survey Ecosystems Mission Area. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature cited

- Alberta Energy. 2016. Energy resources: facts and stats, December 2016. Alberta Energy, Alberta, Canada, <<https://open.alberta.ca/publications/energy-resources-facts-and-stats>> Accessed April 5, 2021.
- Avery, M. L., D. L. Bergman, D. G. Decker, R. D. Flynt, C. E. Knittle, M. A. Pavelka, and K. L. Tope. 1993. Evaluation of aversive conditioning for reducing raven predation on eggs of California least terns, Camp Pendleton, California–1992. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Denver Wildlife Research Center, Denver, Colorado, USA.
- Bell, C. B. 2011. Nest site characteristics and nest success of translocated and resident greater sage grouse at Clear Lake National Wildlife

- Refuge. Thesis. Humboldt State University, Arcata, California, USA.
- BirdLife International. 2019. Bird species distribution maps of the world. Version 2019.1. BirdLife International, Cambridge, United Kingdom, <<http://datazone.birdlife.org/species/request-dis>>. Accessed March 16, 2020.
- Boarman, W. I. 2003. Managing a subsidized predator population: reducing common raven predation on desert tortoises. *Environmental Management* 32:205–217.
- Boarman, W. I., and S. J. Coe. 2002. An evaluation of the distribution and abundance of common ravens at Joshua Tree National Park. *Bulletin of Southern California Academy of Sciences* 101:86–103.
- Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). Pages 1–32 in A. Poole and F. Gillis, editors. *The birds of North America*. Philadelphia, Pennsylvania, USA.
- Boarman, W. I., M. A. Patten, R. J. Camp, and S. J. Collis. 2006. Ecology of a population of subsidized predators: common ravens in the central Mojave Desert, California. *Journal of Arid Environments* 67:248–261.
- Brussee, B. E., and P. S. Coates. 2018. Reproductive success of common ravens influences nest predation rates of their prey: implications for egg-oiling techniques. *Avian Conservation and Ecology* 13(1):17.
- Bui, T.-V. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. *Condor* 112:65–78.
- Coates, P. S., B. E. Brussee, K. B. Howe, K. B. Gustafson, M. L. Casazza, and D. J. Delehanty. 2016. Landscape characteristics and livestock presence influence common ravens: relevance to greater sage-grouse conservation. *Ecosphere* 7:e01203.
- Coates, P. S., J. W. Connelly, and D. J. Delehanty. 2008. Predators of greater sage-grouse nests identified by video monitoring. *Journal of Field Ornithology* 79:421–428.
- Coates, P. S., S. M. Harju, S. J. Dettenmaier, J. B. Dinkins, P. J. Jackson, and M. P. Chenaille. 2021a. Trend estimates of common raven populations in the United States and Canada, 1966–2018: U.S. Geological Survey data release, <https://doi.org/10.5066/P99CNYHP>.
- Coates, P. S., K. B. Howe, M. L. Casazza, and D. J. Delehanty. 2014a. Common raven occurrence in relation to energy transmission line corridors transiting human-altered sagebrush steppe. *Journal of Arid Environments* 111:68–78.
- Coates, P. S., K. B. Howe, M. L. Casazza, and D. J. Delehanty. 2014b. Landscape alterations influence differential habitat use of nesting buteos and ravens within sagebrush ecosystem: implications for transmission line development. *Condor* 116:341–356.
- Coates, P. S., S. T. O’Neil, B. E. Brussee, M. A. Ricca, P. J. Jackson, J. B. Dinkins, K. B. Howe, A. M. Moser, L. J. Foster, and D. J. Delehanty. 2020. Broad-scale impacts of an invasive native predator on a sensitive native prey species within the shifting avian community of the North American Great Basin. *Biological Conservation* 243:e108409.
- Coates, P. S., B. G. Prochazka, M. S. O’Donnell, C. L. Aldridge, D. R. Edmunds, A. P. Monroe, M. A. Ricca, G. T. Wann, S. E. Hanser, L. A. Wiechman, and M. P. Chenaille. 2021b. Range-wide greater sage-grouse hierarchical monitoring framework: implications for defining population boundaries, trend estimation, and a targeted annual warning system. U.S. Geological Survey Open File Report 202-1154.
- Coates, P. S., W. C. Webb, S. J. Dettenmaier, S. M. Harju, and D. J. Delehanty. 2021c. Synthesis of nest predation impacts of common ravens on sensitive avian species. *Human–Wildlife Interactions* 15(3).
- Commission for Environmental Cooperation. 1997. *Ecological regions of North America: towards a common perspective*. Commission for Environmental Cooperation, Montreal, Quebec, Canada, <https://gaftp.epa.gov/EPADDataCommons/ORD/Ecoregions/cec_na/CEC_NAeco.pdf>. Accessed January 4, 2022.
- Conover, M. R., and A. J. Roberts. 2017. Predators, predator removal, and sage-grouse: a review. *Journal of Wildlife Management* 81:7–15.
- Cooper, D. M., E. L. Kershner, and D. K. Garcelon. 2005. The use of shock collars to prevent island fox (*Urocyon littoralis*) predation on the endangered San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*). Sixth California Islands Symposium, Institute for Wildlife Studies, Arcata, California, USA.
- Cramp, S., C. M. Perrins, and D. J. Brooks. 1994. *The birds of the western Palearctic*. Volume 8. Crows to finches. *Handbook of the Birds of*

- Europe, the Middle East, and North Africa: the birds of the Western Palearctic. Oxford University Press, Oxford, United Kingdom.
- Dinkins, J. B., M. R. Conover, C. P. Kirol, J. L. Beck, and S. N. Frey. 2016. Effects of common raven and coyote removal and temporal variation in climate on greater sage-grouse nesting success. *Biological Conservation* 202:50–58.
- Dinkins, J. B., L. R. Perry, J. L. Beck, and J. D. Taylor. 2021. Increased abundance of the common raven within the ranges of greater and Gunnison sage-grouse: influence of anthropogenic subsidies and fire. *Human–Wildlife Interactions* 15(3).
- Eggert, L. S., N. I. Mundy, and D. S. Woodruff. 2004. Population structure of loggerhead shrikes in the California Channel Islands. *Molecular Ecology* 13:2121–2133.
- Ellis, K. S., J. F. Cavitt, and R. T. Larsen. 2015. Factors influencing snowy plover (*Charadrius nivosus*) nest survival at Great Salt Lake, Utah. *Waterbirds* 38:58–67.
- Ellis, K. S., R. T. Larsen, and D. N. Koons. 2020. Dependence of spatial scale in landscape associations with cause-specific predation of snowy plover nests. *Ecosphere* 11:e03257.
- Engel, K. A., and L. S. Young. 1992. Movements and habitat use by common ravens from roost sites in southwestern Idaho. *Journal of Wildlife Management* 56:596–602.
- Engel, K. A., L. S. Young, K. Steenhof, J. A. Roppe, and M. N. Kochert. 1992. Communal roosting of common ravens in southwestern Idaho. *Wilson Bulletin* 104:105–121.
- Fleischer, R. C., W. I. Boorman, E. G. Gonzalez, A. Godinez, K. E. Omland, S. Young, L. Helgen, G. Syed, and C. E. McIntosh. 2008. As the raven flies: using genetic data to infer the history of invasive common raven (*Corvus corax*) populations in the Mojave Desert. *Molecular Ecology* 17:464–474.
- Fox, A. D., J. Madsen, H. Boyd, E. Kuijken, D. W. Norriss, I. M. Tombre, and D. A. Stroud. 2005. Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. *Global Change Biology* 11:881–893.
- Frost, N. 2014. California least tern breeding survey: 2013 season. California Department of Fish and Game, Habitat Conservation and Planning Branch, Species Conservation and Recovery Program Report 1.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–472.
- Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and habitats*. Volume 38. *Studies in avian biology*. University of California Press, Berkeley, California, USA.
- Hamer, T. E., and S. K. Nelson. 1995. Nesting chronology of the marbled murrelet. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California, USA.
- Hanks, L. M., J. D. Barbour, K. Kratz, and W. C. Webb. 2009. Ad libitum water source for a common raven. *Wilson Journal of Ornithology* 121:210–212.
- Harju, S. M., C. V. Olson, J. E. Hess, and B. Bedrosian. 2018. Common raven movement and space use: influence of anthropogenic subsidies within greater sage-grouse nesting habitat. *Ecosphere* 9:e02348.
- Howe, K. B., P. S. Coates, and D. J. Delehanty. 2014. Selection of anthropogenic features and vegetation characteristics by nesting common ravens in the sagebrush ecosystem. *Condor* 116:35–49.
- Kelly, J. P., K. L. Etienne, and J. E. Roth. 2002. Abundance and distribution of the common raven and American crow in the San Francisco Bay Area, California. *Western Birds* 33:202–217.
- Knight, R. L., R. J. Camp, and H. A. L. Knight. 1998. Ravens, cowbirds, and starlings at springs and stock tanks, Mojave National Preserve, California. *Great Basin Naturalist* 58:393–395.
- Knight, R. L., and J. Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. *Journal of Wildlife Management* 57:266–271.
- Knight, R. L., H. A. Knight, and R. J. Camp. 1993. Raven populations and land-use patterns in the Mojave Desert, California. *Wildlife Society Bulletin* 21:469–471.
- Kristan, W. B., and W. I. Boorman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. *Ecology* 84:2432–2443.
- Kristan, W. B., and W. I. Boorman. 2007. Effects of anthropogenic developments on common raven nesting biology in the west Mojave Desert. *Ecological Applications* 17:1703–1713.

- Lauten, D. J., K. A. Castelein, S. Weston, K. Eucken, and E. P. Gaines. 2006. The distribution and reproductive success of the western snowy plover along the Oregon coast—2006. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications* 18:1119–1139.
- Liebezeit, J. R., and T. L. George. 2002. A summary of predation by corvids on threatened and endangered species in California and management recommendations to reduce corvid predation. California Department of Fish and Game, Species Conservation and Recovery Program Report 2002-02.
- Link, W. A., J. R. Sauer, and D. K. Niven. 2017. Model selection for the North American Breeding Bird Survey: a comparison of methods. *Condor* 119:546–556.
- Littlefield, C. D. 1995. Sandhill crane nesting habitat, egg predators, and predator history on Malheur National Wildlife Refuge, Oregon. *Northwestern Naturalist* 76:137–143.
- Littlefield, C. D. 1999. Greater sandhill crane productivity on privately owned wetlands in eastern Oregon. *Western Birds* 60:206–210.
- Littlefield, C. D. 2003. Sandhill crane nesting success and productivity in relation to predator removal in southeastern Oregon. *Wilson Bulletin* 115:263–269.
- Lockyer, Z. B., P. S. Coates, M. L. Casazza, S. P. Espinosa, and D. J. Delehanty. 2013. Greater sage-grouse nest predators in the Virginia Mountains of northwestern Nevada. *Journal of Fish and Wildlife Management* 4:242–254.
- Manly, A., F. L. Waterhouse, and A. S. Harestad. 1999. Nesting habitat of marbled murrelets on the Sunshine Coast. Forest Research Extension Note. British Columbia Ministry of Forests, British Columbia, Canada.
- Marschalek, D. A. 2011. California least tern breeding survey, 2010 season. California Department of Fish and Game, Habitat Conservation and Planning Branch, Species Conservation and Recovery Program Report 1.
- Marzluff, J. M., and E. Neatherlin. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological Conservation* 130:301–314.
- Mee, A., and N. F. Snyder. 2007. California condors in the 21st century—conservation problems and solutions. Pages 243–279 in A. Mee, L. S. Hall, and J. Grantham, editors. *California condors in the 21st century*. Series in Ornithology, No. 2. American Ornithologists Union, Washington, D.C., and Nuttall Ornithological Club, Cambridge, Massachusetts, USA.
- Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. *Journal of Wildlife Management* 71:1773–1783.
- Omernik, J. M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* 77:118–125.
- O’Neil, S. T., P. S. Coates, B. E. Brussee, P. J. Jackson, K. B. Howe, A. M. Moser, L. J. Foster, and D. J. Delehanty. 2018. Broad-scale occurrence of a subsidized avian predator: reducing impacts of ravens on sage-grouse and other sensitive prey. *Journal of Applied Ecology* 55:2641–2652.
- Pardieck, K. L., D. J. Ziolkowski, Jr., M. Lutmerding, V. I. Aponte, and M.-A. R. Hudson. 2020. North American Breeding Bird Survey dataset 1966–2019: U.S. Geological Survey data release, Washington D.C., USA.
- Parson, S., and E. Ray. 2016. Sustainable colonization: tar sands as resource colonialism. *Capitalism Nature Socialism* 29:68–86.
- Peebles, L. W., and M. R. Conover. 2017. Winter ecology and spring dispersal of common ravens in Wyoming. *Western North American Naturalist* 77:293–308.
- Peebles, L. W., M. R. Conover, and J. B. Dinkins. 2017. Adult sage-grouse numbers rise following raven removal or an increase in precipitation. *Journal of Wildlife Management* 41:471–478.
- Sauer, J. R., and W. A. Link. 2011. Analysis of the North American Breeding Bird Survey using hierarchical models. *Auk* 128:87–98.
- Sauer, J. R., K. L. Pardieck, D. J. Ziolkowski, A. C. Smith, M.-A. R. Hudson, V. Rodriguez, H. Berlanga, D. K. Niven, and W. A. Link. 2017. The first 50 years of the North American Breeding Bird Survey. *Condor* 119:576–593.
- Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon, and A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology* 12:564–575.
- Singer, S. W., N. L. Naslund, S. A. Singer, and C. J. Ralph. 1991. Discovery and observations of

- two tree nests of the marbled murrelet. *Condor* 93:330–339.
- Smith, A. P., and D. G. Quin. 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* 77:243–267.
- Steenhof, K., M. N. Kochert, and J. A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. *Journal of Wildlife Management* 57:271–281.
- Stern, M. A., G. J. Pampush, and R. E. D. Carlo. 1987. Nesting ecology and productivity of greater sandhill cranes at Sycan Marsh, Oregon. Pages 249–256 in *Proceedings of the 1985 International Crane Workshop*. U.S. Fish and Wildlife Service, Grand Island, Nebraska, USA.
- Taylor, J. D., R. D. Holt, E. K. Orning, and J. K. Young. 2017. Greater sage-grouse nest survival in northwestern Wyoming. *Journal of Wildlife Management* 81:1219–1227.
- Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management* 76:336–347.
- Webb, W. C., W. I. Boarman, and J. T. Rotenberry. 2004. Common raven juvenile survival in a human-augmented landscape. *Condor* 106:517–528.
- Webb, W. C., W. I. Boarman, and J. T. Rotenberry. 2009. Movements of juvenile common ravens in an arid landscape. *Journal of Wildlife Management* 73:72–81.
- Webb, W. C., J. M. Marzluff, and J. Hepinstall-Cymerman. 2011. Linking resource use with demography in a synanthropic population of common ravens. *Biological Conservation* 144:2264–2273.
- White, C. M., and M. Tanner-White. 1988. Use of interstate highway overpasses and billboards for nesting by the common raven (*Corvus corax*). *Great Basin Naturalist* 48:64–67.

Associate Editor: Terry A. Messmer

SETH M. HARJU is a biometrician and research biologist who works on wildlife issues across the western United States, recently including raven ecology and impacts to prey species, Mojave desert tortoise ecology and recovery, endangered beetle population estimation, pronghorn resource selection, elk and sage-grouse response to energy development, and several other interesting projects. He received his B.S. degree from the University of Idaho (2003) and M.S. degree from Utah State University (2007). Along with his wife and 2 kids, he enjoys quasi-homesteading and roaming the Northern Rockies.



PETER S. COATES is a research wildlife biologist for the U.S. Geological Survey, Western Ecological Research Center. He obtained a Ph.D. degree from Idaho State University and an M.S. degree from University of Nevada Reno. His research currently focuses on population ecology of greater sage-grouse and other sensitive prey species. Specifically, he investigates relationships between species' habitat, predators, and climate. His studies also focus on how anthropogenic-resource subsidies influence changes in raven and other predator populations. His research findings are intended to help inform management practices and guide resource policies using quantitative decision support tools.



SETH J. DETTENMAIER is a noteworthy wildlife biologist with the U.S. Geological Survey. He earned his B.S. degree in conservation ecology and a Ph.D. degree in wildlife ecology from Utah State University. He is passionate about conservation of our natural resources and providing tools to help others achieve the same. He recently discovered statistics that show 47% of people are pedantic. Well, 46.8%.



JONATHAN B. DINKINS is an assistant professor in the Department of Animal and Rangeland Sciences at Oregon State University. His position is focused on shrub-steppe wildlife ecology, which includes research and outreach through Extension. His interests include topics related to animal behavior, population dynamics, predator-prey dynamics, wildlife habitat use, and human-wildlife interactions. During the past decade, he has worked on quantitative research projects focused on wildlife habitat use and demography in relation to habitat condition, predator effects on site selection of prey, predator effects on prey vital rates, and wildlife habitat related to anthropogenic development.



Authors continued on next page...

PAT J. JACKSON graduated from the University of Missouri in 2007 with a bachelor's degree in forestry



and another bachelor's degree in fisheries and wildlife. After graduation, he enjoyed a short stint of wildlife field work in southeast Alaska, transitioned to full-time trapping in Missouri, and then moved to Hawaii in 2008. In Hawaii, he spent

2 years doing vertebrate pest work focusing on feral cats, rats, and feral swine removal. In 2010, he moved to Utah and began work on a Ph.D. degree focusing on coyote biology, diet, and home ranges in central Nevada. He is currently the predator management staff specialist for Nevada Department of Wildlife. His professional interests include wildlife damage management, animal capture techniques, best management practices for furbearer trapping, public outreach, and predator management. He is an avid trapper, fisherman, and hunter, primarily focusing on big game in the west. One of his favorite aspects involves teaching others to big game hunt and trap. He also thoroughly enjoys sharing and teaching others to butcher and prepare wild game.

MICHAEL P. CHENAILLE is a cartographic technician with the U.S. Geological Survey's Western



Ecological Research Center in Dixon, California. He holds a B.A. degree in geology from Humboldt State University and an A.S. degree in geographic information systems from American River College; he provides expertise on geospatial methodologies and applications.

His work primarily focuses on the greater sage-grouse and sagebrush ecosystems of the Great Basin region of the western United States. In his free time, he enjoys sandwiches and short walks on long beaches.