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Synthesis

Occurrence, resource use, and demography of the common raven in North America: a research synthesis

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Abstract: We reviewed the scientific literature to inventory existing studies of common raven (*Corvus corax*; raven) ecology in western North America. We conducted an intial literature review between June 2015 and March 2018. Prior to completing our review, we revisited the published literature for any additional relevant studies in July 2021. Our goal was to identify knowledge gaps and to synthesize the current understanding of environmental features that may support raven populations that pose general threats to biodiversity and sensitive species in particular. We focused our review on studies with direct conservation applications related to 3 processes of raven ecology: occurrence, resource use, and demography. We identified covariates that researchers associated with these processes of raven ecology, and we also quantified the geographic distribution of studies. Our review identified 54 studies, with an increasing number of studies published per decade and a geographic bias characterized by more studies conducted in the Mojave and Columbia Plateau ecoregions than elsewhere. Most studies (44) reported on a single ecological process, but 10 studies reported on multiple ecological processes. Results related to raven occurrence appeared 31 times; demographic results appeared 21 times; and resource use was reported 17 times. We also identified 13 explanatory covariates regularly invoked to explain variation in raven ecological processes. Greater attention was given to covariates including vegetation land cover, human settlement, recreation, and linear rights-of-ways than were used to explain variation in ecological processes. Most demographic studies investigated raven reproduction exclusively, but a small number of studies considered raven survival exclusively or in combination with reproduction. Along with a detailed summary of individual studies provided as an appendix, we intend for our findings to serve as a reference and to help identify future research priorities.

Key words: anthropogenic subsidies, common raven, *Corvus corax,* demography, literature review, management, occurrence, research priorities, resource use

The ecology of common ravens (*Corvus corax;* ravens) in western North America has received much scientific attention in recent decades. In particular, negative impacts of growing raven populations on sensitive species and western ecosystems have motivated interest in management of raven populations. Many studies now have demonstrated that raven populations respond positively to anthropogenic resource subsidies from expanding human enterprise in the American West (Kristan and Boarman 2007, Webb et al. 2011). Increased raven abundance and range expansion impact sensitive species in a variety of ways including directly through predation on eggs or young (Kristan and Boarman 2003, Coates et al. 2008, Ellis et al. 2020) and indirectly through interspecific territorial interactions (Marzluff and Heinrich 1991, Boarman and Heinrich 1999, Freeman and Miller 2018). The continued growth of human enterprise in western North America (Leu et al. 2008) likely portends increasing negative impacts of ravens on sensitive species and western ecosystems.

We reviewed the scientific literature on studies of ravens and studies implicating ravens as

a source of ecological perturbation. Our review primarily covered studies that were conducted in western North America where raven population growth is a conservation concern (Kristan and Boarman 2003, Coates et al. 2020). Our primary objective was to describe the current state of knowledge about raven ecology in western North America and idenify areas where scientific information is lacking. We hypothesized that we would find disproportionately high treatment of raven ecology relative to other areas of investigation, such as raven diet. Also, we predicted that the number of studies would reflect a geographic bias toward ecoregions most impacted by growing raven populations. Lastly, we predicted the types of studies would reflect the relative difficulty in collecting certain types of ecological data. Herein, we provide a summary of peer-reviewed literature on raven occurence, resource use, and demography to serve as a reference for raven management and to highlight information gaps and guide future research.

Methods

Defining geographical boundaries and types of literature

We restricted our raven occurrence, resource use, and demography literature search to scientific studies conducted in western North America and Greenland. We defined western North America as those portions of the continent west of the 95° meridian. We searched only primary sources in the peer-reviewed scientific literature, which included research articles, book chapters, review papers, and short communications. We used the online Google Scholar search engine using "*Corvus corax*," followed by any terms related to occurrence, resource use, or demography (e.g., "*Corvus corax* survival"). We conducted our initial literature review between June 2015 and March 2018. Prior to completing the review, we revisited the literature in July 2021 for any additional relevant published studies.

Categorizing studies

We categorized studies as describing 1 of 3 aspects of raven biology: (1) studies of raven occurrence, occupancy, or distribution (hereafter, occurrence); (2) studies of raven resource use, including studies relating spatial distribution with 1 or more covariates and studies self-described as investigations of habitat selection, habitat use, and/or resource use except for those studies focused on raven diet); and (3) studies involving raven demography (hereafter, demography). We considered all studies, including original research efforts related to at least 1 of these aspects of raven biology. Categorizing studies sometimes required subjective judgment, but we attempted to portray the literature accurately based on the ecological processes under study in each work.

We excluded studies of raven diet, foraging behavior, and predation. These direct impacts by ravens are of great importance but fall beyond the scope of our review of raven occurance, resource use, and demography. We also excluded studies focused primarily on raven behavioral ecology or interspecific interactions as beyond our scope.

We used a range of attributes to categorize individual studies. Studies of raven occurrence or distribution were studies that reported on patterns of abundance and/or density of ravens, often in relation to 1 or more environmental feature. Studies of environmental features were those that considered the suite of physical and biological components in the environment associated with occupancy locations by ravens (Webb et al. 2011). For example, many studies employed point count census data that described the relative probability of occurrence within a study area (e.g., on a grid design within a Geographic Information Systems framework).

We categorized studies as being concerned with raven resource use if they combined occurrence or density data with relative measures of use or other information connecting ravens with specific environmental features. Methods employed in resource use studies varied but often involved behavioral observations, sometimes involving marked individuals. In some studies, resource use was directly observed. In other studies, it was inferred by geospatial analyses. Some studies met our resource use criteria by generating models of use from occurrence data; others did so through intensive tracking of marked individuals. We also included several studies that were somewhat anecdotal but reported on the specific use of environmental features. We also included studies that found resource use associations by employing geo-

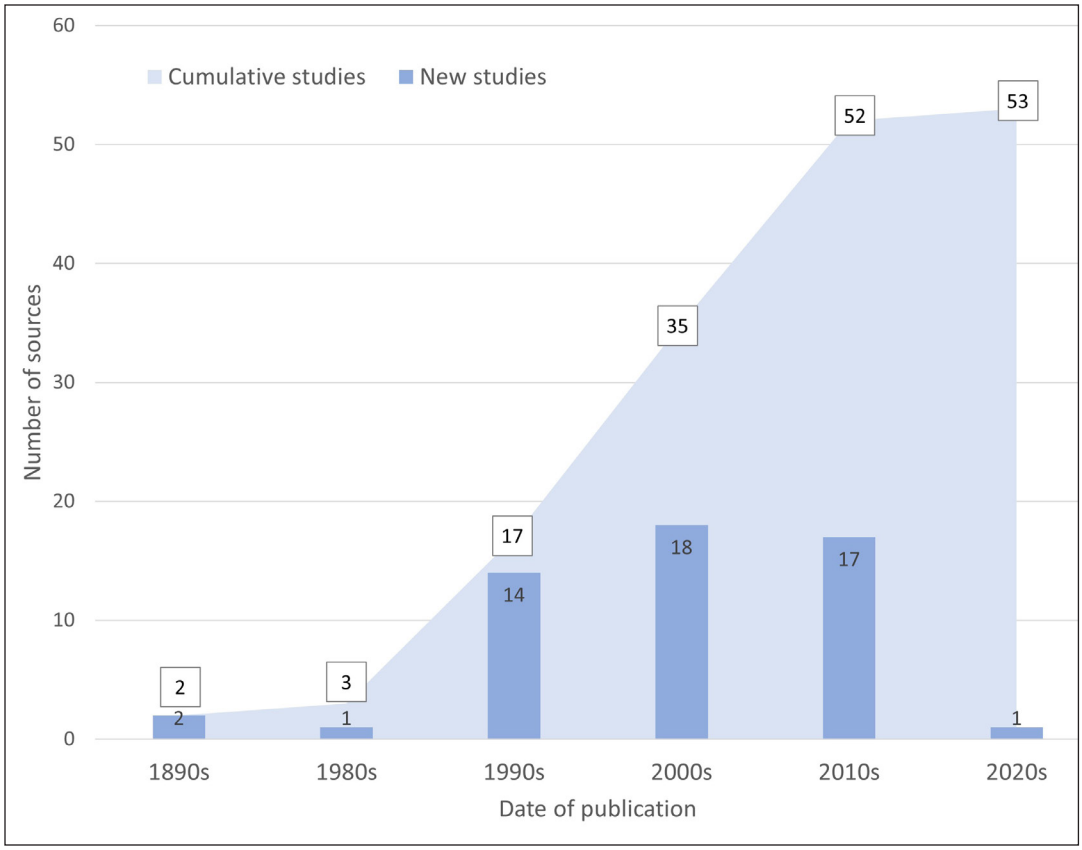

Figure 1. The number of sources describing common raven (*Corvus corax*) ecology in western North America and Greenland and the decade of publication. We conducted an initial literature review between June 2015 and March 2018. In July 2021, prior to completing the project, we conducted a second review of the literature for any additional relevant published studies.

spatial analysis to extrapolate occurrence data and generate models of relative abundance across a landscape using analytical techniques such as resource selection functions. Summaries of the findings of these studies appear in the supplemental material (Appendix A).

Spatial extent and description

We restricted our search to studies conducted within the geographical boundary defined by North America. We described locations using The Nature Conservancy's ecoregions (Groves et al. 2002) for those studies occurring within the contiguous United States. In 1 study in Alaska, USA (Baltensperger et al. 2013), we describe its location using the United States Environmental Protection Agency's ecoregions (Omernik 1995). We also included 1 study in southwestern Greenland (Restani et al. 2001) using ecoregion descriptions published by the World Wildlife Fund (Olson et al. 2001).

Results

We identified 54 studies of raven ecology with relevance to raven occurrence, resource use, or demography in North America. Most studies were research articles (81%; 44 studies), followed by short communications (13%; 7 studies), and reviews or book chapters (6%; 3 studies). Ravens were the primary focus in most sources (89%; 48 studies). We documented relevant information from 3 studies (5%) investigating corvid communities and 3 studies (5%) investigating ravens and raptors.

Studies of raven ecology in North America were virtually nonexistent or not accessible before the late 1980s, apart from 2 short communications published in 1899. In the 1990s, 14 new studies were published, starting a trend of increasing attention to raven ecology in North America in the scientific literature. In the following decade, 18 studies were published, with an additional 18 since that time (Figure 1). The

Table 1. Frequency of ecological processes and ecoregions studied in common raven (*Corvus corax*; raven) ecology studies conducted in western North America and Greenland. We conducted our initial literature review between June 2015 and March 2018. We revisited the literature to search for additional relevant studies published between March 2018 and July 2021. We identified 54 studies of raven ecology with relevance to raven occurrence, resource use, and/or demography in North America.

Ecoregion	Ecological process					
	Occurrence	Resource use	Demography	Topics by ecoregion	# Studies	% Studies
Interior Bottomlands (Alaska Boreal Interior)	1	0	0	1	1	2
North Cascades	1	0	0	1	1	2
Utah High Plateau	0	0	1	1	1	2
California North Coast	1	1	0	2	1	2
Kalaallit Nunaat low Arctic tundra (Greenland)	0	1	1	2	1	2
Wyoming Basins	0	2	0	2	2	4
California Central Coast	3	2	0	5	3	6
Great Basin	2	3	0	5	3	6
California South Coast	0	1	4	5	4	7
West Cascades and Coastal Forests	3	1	3	7	5	9
Utah-Wyoming Rocky Mountains	6	1	3	10	6	11
Columbia Plateau	3	3	5	10	10	19
Mojave Desert	11	2	4	17	16	30
Total	31	17	21	67	54	
% studies where ecological processes considered	57	32	40			

Mojave Desert was the most studied ecoregion (30%; 16 studies), followed by the Columbia Plateau (19%; 10 studies; Table 1). The total number of times 1 of the 3 ecological processes of occurrence, resource use, or demography was addressed per ecoregion was associated with the total number of studies in each ecoregion. For example, studies in the Mojave Desert addressed the 3 topics 17 times (16 studies), and studies in the Columbia Plateau addressed the 3 topics 10 times (10 studies; Table 1). In the West Cascades and Coastal Forests ecoregions, a slightly greater number of topics were addressed relative to the number of studies (7 topics, 5 studies), as also was the case for the Utah-Wyoming (USA) Rocky Mountains region (10 topics, 6 studies).

Most studies (81%; 44) reported a single ecological process, either occurrence, resource use, or at least 1 aspect of demography. Seven studies (13%) reported 2 ecological processes, and 3 studies (6%) reported on all 3 ecological processes. Across these studies, ecological processes appeared a total of 67 times: occurrence was addressed 30 times (56%), resource use 17 times (31%), and demography 21 times (39%; Table 1).

We identified 13 explanatory covariates regularly invoked to explain variation in raven occurrence, resource use, or demography (Tables 2, 3, 4, and 5). We identified 10 additional co-

Table 2. Explanatory covariates invoked to explain variation in common raven (*Corvus corax*) occurrence and resource use in western North America and Greenland. For the identity of numbered sources, see Appendix Table 1. We conducted our initial literature review between June 2015 and March 2018. Prior to completing the project, we revisited the literature for any additional relevant studies published in the interval between March 2018 and July 2021.

Ecological processes	Covariates				
	Age and/or sex	Agriculture	Human settlement and/or structures	Linear right-of-way	Livestock
Occurrence	0	6	7	8	2
Sources – occurrence		9, 10, 11, 24, 28, 37	4, 5, 9, 10, 24, 28, 31	4, 9, 11, 26, 29, 31, 37, 54	10, 24
Resource use	3	3	7	7	4
Sources – resource use	16, 39, 49	14, 15, 48	1, 8, 21, 40, 41, 48, 49	8, 16, 18, 21, 41, 48, 49	15, 40, 48, 49

Table 3. Explanatory covariates invoked to explain variation in common raven (*Corvus corax*) occurrence and resource use in western North America and Greenland. For the identity of numbered sources, see Appendix Table 1. We conducted our initial literature review between June 2015 and March 2018. Prior to completing the project, we revisited the literature for any additional relevant studies published in the interval between March 2018 and July 2021.

Ecological processes	Covariates				
	Other species	Physiography	Point subsidies: landfills, hatcheries, sewage ponds	Recreation	Supplemental water
Occurrence	4	1	3	3	3
Sources – occurrence	5, 9, 25	9	4, 5, 37	27, 51, 52	4, 10, 30
Resource use	2	0	5	0	1
Sources – resource use	35, 40		15, 35, 39, 48, 49		19

Table 4. Explanatory covariates invoked to explain variation in common raven (*Corvus corax*) occurrence and resource use in western North America and Greenland. For the identity of numbered sources, see Appendix Table 1. We conducted our initial literature review between June 2015 and March 2018. Prior to completing the project, we revisited the literature for any additional relevant studies published in the interval between March 2018 and July 2021.

Ecological processes	Covariates		
	Season	Time of day	Vegetation land cover
Occurrence	2	3	8
Sources – occurrence	5, 52	5, 27, 52	4, 7, 9, 17, 28, 30, 37, 41
Resource use	5	2	7
Sources – resource use	1, 14, 15, 16, 19	14, 38	8, 12, 14, 15, 41, 48, 49

variates used to describe variation in reproduction, survival, or both (Table 5). The covariates described environmental features or attributes of individual ravens. Covariates such as vegetation land cover were compared to >1 ecological process in those papers covering multiple ecological processes, and thus the number of comparisons exceeded the number of sources. For example, vegetation land cover was compared to ecological processes 19 times across 17 studies (32%; Tables 2, 3, 4, and 5).

Demography was the second most common-

Table 5. Effects of explanatory covariates on common raven (*Corvus corax*) survival and reproduction in western North America and Greenland. The symbol "+" indicates the source in parentheses is found in a relationship, with either a positive or negative influence on demographic parameters. The symbol "0" means the source did not find a relationship between survival or reproduction and the covariate. The identity of sources indicated by numbers in parenthesis is located in Appendix Table 1. We conducted an initial literature review between June 2015 and March 2018. In July 2021, prior to completing the project, we conducted a second review of the literature for any additional relevant published studies.

Explanatory variables	Survival	Reproduction
Age class/age	+ (47,49)	N/A
Air temperature	N/A	+ (47)
Agriculture	N/A	N/A
Body condition	0 (47)	N/A
Diet	N/A	+ (31)
Fledging date	+ (47)	N/A
Fledging year	+ (47)	N/A
Human settlement and/or structure	+ (36, 48, 49)	+ (32, 36, 49)
Landscape configuration	+ (49)	+ (49)
Laying date	N/A	+ (13, 32)
Linear rights-of-way	0 (47); + (49)	+ (32, 49)
Livestock	+ (47)	N/A
Movement	+ (39)	N/A
Nest substrate	N/A	+, 0 (32); + (43)
Other species	+ (36, 39, 47, 49)	N/A
Physiography	N/A	+ (32)
Point subsidies	+ (47, 49)	+ (32, 49)
Recreation	+ (36)	+ (36, 52)
Season	N/A	N/A
Sex	0 (47, 49)	N/A
Transmitter attachment	0 (47)	N/A
Vegetation land cover	+ (49)	+ (13, 32, 49)
Water	N/A	+ (32)
Total studies	5	8

ly reported ecological process describing raven ecology (21 studies; 39%; Table 1). Among the papers discussing demography, 17 (81%) described reproduction, and 2 of these also included survival data. Two additional studies reported survival data only (Table 6). Reproduction was studied in 6 of the 11 geographical regions, and survival was reported in just 3 regions (Table 6).

Below we provide a synopsis of the literature on raven ecology in western North America. Specifically, we summarize the relationships between occurrence, resource use, and demography with reported explanatory covariates. Some articles addressed 1 or more ecological processes with multiple covariates, and thus we considered those papers in our analyses more than once. Details supporting our synopsis are provided in the supplemental material (Appendix A).

Synopsis of ecological processes and explanatory covariates

Vegetation land cover. Our consideration of the vegetation land cover covariate included the full range of land cover and landuse types within a study area or the reported configuration of these landscape components. In some cases, the land uses include agriculture, which we address separately due to its prominent role in providing subsidies to raven populations. Studies report that raven occurrence and resource use frequently are higher in fragmented or human-modified vegetation land cover and lower in undisturbed vegetation landscapes (Engel and Young 1992*a*; Camp et al. 1993; Knight et al. 1998; Boarman and Coe 2002; Webb et al. 2009, 2011; Coates et al. 2014*a*; Howe et al. 2014). Ravens use habitat edges and patchy land cover configurations, and relative occurrence or occupancy increases in these types of landscapes (Gaines et al. 2010, Webb et al. 2011, Scarpignato and George 2013, Coates et al. 2014*b*, Howe et al. 2014, O'Neil et al. 2018). Surrounding land cover and/or structural complexity influences raven reproduction, with ravens selecting nest sites closer to habitat edges than random (Kristan and Boarman 2007, Howe et al. 2014).

Human settlement and/or structures. Raven abundance or resource use is elevated near human settlements such as municipalities, military bases, and energy facilities (Knight et al. 1993; Boarman and Coe 2002; Kelly et al. 2002; Kristan and Boarman 2003; Roth et al. 2004;

Table 6. Common raven (*Corvus corax*) demographic studies related to reproduction and/or survival by ecoregion in western North America and Greenland. See Appendix Table 1 for sources indicated by numbers. We conducted an initial literature review between June 2015 and March 2018. In July 2021, prior to completing the project, we conducted a second review of the literature for any additional relevant published studies.

Ecoregion	Reproduction		Survival	
	Source	Focus	Source	Focus
California South Coast	34*	Substrate		
	35*	Substrate, productivity, nest density		
	44	Substrate, nest microhabitat, productivity		
	46*	Substrate, # broods		
Columbia Plateau	43	Substrate, productivity		
	53*	Substrate		
	8	Substrate, nest density, land use, land cover		
	51	Substrate, nest density, land use, land cover		
Greenland			39	Age groups, band recoveries
Mojave Desert	31	Land use	47	Juveniles, radio-tracking
	32	Substrate, productivity, land use, land cover, laying date, clutch size, nest size occupancy, nest distribution, breeding initiation		
	33	Productivity, diet		
Utah High Plateau	23*	Substrate		
Utah-Wyoming Rocky Mountains	6	Substrate		
	13*	Substrate, productivity, land cover, laying date		
	52	Nest density		
West Cascades and Coastal Forests	36	Productivity, brood size	36	Adults, radio-tracking
	49	Productivity, resource use	49	All age groups, radio-tracking, sexes, resource use
Total reports	17		4	

* Short communication, observation, or note

Webb et al. 2009, 2011; Baltensperger et al. 2013; Scarpignato and George 2013; Coates et al. 2014*a*, 2016; Peebles and Conover 2017). Raven reproduction and survival also are elevated near human settlement (Webb et al. 2004, Marzluff and Neatherlin 2006, Kristan and Boarman 2007, Webb et al. 2011).

Ravens readily use anthropogenic structures for nesting such that the introduction of these structures increases available nesting substrate for ravens compared to undisturbed habitat. Structures include buildings, powerline transmission towers, communication towers, and bridges (Webb and Ellstrand 2003, Kristan and

Boarman 2007, Bui et al. 2010, Coates et al. 2014*b*, Howe et al. 2014, Peebles and Conover 2017, Harju et al. 2018). Natural nesting substrates include cliffs and trees (Linton 1899, Linz et al. 1992, Kristan and Boarman 2007, Sullivan et al. 2011, Coates et al. 2014*b*, Howe et al. 2014).

Linear rights-of-way (LROW). Most studies found elevated raven occurrence, resource use, and density in proximity to linear rights-of-way (Knight and Kawashima 1993; Knight et al. 1995; Boarman and Coe 2002; Webb et al. 2009, 2011; Scarpignato and George 2013; Coates et al. 2014*b*, 2016; Gibson et al. 2018; O'Neil et al. 2018; Coates et al. 2020). However, distance to roads did not influence raven counts conducted by Kristan and Boarman (2003). Ravens frequently use LROW infrastructure, such as powerline transmission tower cross members, as roosting (Engel and Young 1992*a*, Restani and Lueck 2020) 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. 2014*b*, Howe et al. 2014, Peebles and Conover 2017, Harju et al. 2018).

Roads influenced raven demographic parameters. For example, nest productivity is increased by proximity to roads (Kristan and Boarman 2007) and adult use of roads (Webb et al. 2011). However, the use of roads also has been associated with lower survival (Webb et al. 2011), and juveniles fledging from nests closer to human activities are more likely to die from an anthropogenic source of mortality than from a natural source of mortality (Webb et al. 2004).

Point subsidies: landfills, hatcheries, sewage ponds. Landfills, sewage ponds, hatcheries, and other point subsidies function as attractants for ravens (Engel and Young 1992*b*; Restani et al. 2001; Boarman and Coe 2002; Boarman et al. 2006; Webb et al. 2009, 2011; Peebles and Conover 2017; Harju et al. 2018; O'Neil et al. 2018). Point subsidies influence raven demographic parameters substantially. For example, nest proximity to point subsidies is associated with increased nest productivity (Kristan and Boarman 2007) and juvenile survival (Webb et al. 2004). In addition, raven use of point subsidies is associated with increased survival (Webb et al. 2011, Peebles and Conover 2017).

Livestock. Several studies specifically addressed livestock production, including some that also considered other land use categories. In these studies, increased raven occurrence and resource use is associated with livestock and confined feeding operations (Engel and Young 1992*a*; Kelly et al. 2002; Roth et al. 2004; Webb et al. 2009, 2011; Coates et al. 2016).

Recreation. Increased raven occurrence and resource use are associated with forms of outdoor recreation that provide supplemental food, such as fishing (Knight et al. 1991) and hunting (White 2005, 2006). Raven survival and reproduction are elevated in proximity to outdoor recreation (Marzluff and Neatherlin 2006, White 2006).

Agriculture. Several studies specifically addressed agriculture, including some that also considered other land use categories. In these studies, increased raven occurrence and resource use is associated with agriculture (Engel and Young 1992*b*, Knight et al. 1993, Kelly et al. 2002, Webb et al. 2009, Coates et al. 2016, O'Neil et al. 2018, Coates et al. 2020).

Supplemental water. Anthropogenic sources of water other than sewage ponds can influence raven occurrence. In arid ecoregions, increased raven occurrence and resource use is associated with supplemental surface water (Knight et al. 1998, Boarman and Coe 2002, Hanks et al. 2009, Coates et al. 2016, O'Neil et al. 2018).

Season and date. Eight studies found fluctuation in raven seasonal abundance and raven resource use to be correlated with supplemental food availability (Restani et al. 2001, White 2006, Baltensperger et al. 2013, Peebles and Conover 2017), seasonal weather patterns (Restani et al. 2001, Baltensperger et al. 2013), or or correlated to raven reproductive timing (Engel and Young 1992*a*, *b*; Engel et al. 1992; Restani et al. 2001; Boarman et al. 2006). However, later egg laying and fledging dates are associated with reduced raven nest productivity (Dunk et al. 1997, Kristan and Boarman 2007) and juvenile survival (Webb et al. 2004).

Age and sex. Older ravens and those with a breeding territory exhibit higher survival than juveniles, subadults, and nonbreeding/nonterritorial ravens (Restani et al. 2001, Webb et al. 2004, Marzluff and Neatherlin 2006, Webb et al. 2011). Furthermore, males and females of the same age exhibit similar rates of survival (Webb et al. 2004, 2011).

Discussion

Our review of raven studies, which addressed raven occurrence, raven resource use, and raven demography, revealed several patterns in the prevailing literature. We found strong geographic trends in the locations of study. Ravens of the Mojave ecosystem have received much attention in the literature (16 studies), undoubtedly driven by concern over the impacts of ravens on desert tortoise (*Gopherus agassizii*) populations. Similarly, ravens within the sagebrush habitats of the Columbia Plateau have received significant recent investigation (10 studies), substantially driven by the impacts of ravens on declining sage-grouse (*Centrocercus urophasianus*) populations. These 2 ecoregions hosted 49% of the studies reviewed, and raven research continues in these regions. In contrast, 5 of 13 ecoregions had just a single study. Importantly, geographic skew in study locations could potentially bias conclusions about raven ecology by failing to adequately represent geographic variation in raven ecology. Raven ecology undoubtedly merits much further study in those ecoregions where it has not received much attention.

Across the studies we reviewed, 13 covariates were invoked as explanatory for raven ecological processes. For example, ravens were regularly observed to exhibit strong associations with anthropogenic factors and structures. Most of these findings, however, emanate from arid ecosystems and sagebrush (*Artemisia* spp.) habitats. It is important for investigators and managers to be aware that geographic skew in published studies also could skew the emphasis of particular explanatory covariates such anthropogenic structures. Covariates such as this may not represent patterns in other parts of North America due to differences in the availability of habitat resources among regions. Ravens are highy adaptable with vast occupany across the Northern Hemisphere within which they use environments ranging from from arctic to desert habitats. Many regionally significant environmental covariates likely have not yet been identified in the literature due to lack of sufficient investigation in many regions.

The geographic skew in the literature likely is constricting our broad understanding of raven ecology. Nevertheless, investigations in well represented regions in western North America point strongly to deleterious interactons between ravens and sensitive species and indicate a need for raven management if sensitive species are to be well protected into the future. One outcome of the strong evidence identifying anthropogenic covariates in Mojave and the Columbia Plateau is highlighting the need for applied research investing our ablity to implement effective protection from ravens for sensitive species based on known environmental relationships. In scientifically underrepresented regions, our results call for basic research to identify environmental factors associated with elevated raven numbers and their impacts on sensitive species.

In addition to geographic skew, we found a disproportionate number of studies addressing 3 ecological processes. This may reflect difficulty in acquiring different types of data. Not surprisingly, studies of raven occurrence were the most common (30 studies; 57%) as these data are relatively easy to obtain in the form of presence or absence data at survey points or transects. Only 1 study related anthropogenic and environmental covariates to raven densities across multiple sites, which required more robust distance-based sampling methodology and accounting for imperfect detection (Buckland et al. 2001). Studies collecting demographic data were almost as numerous (21 studies; 40%), but 17 of 21 (81%) of these focused on reproduction. In most altricial birds, reproductive data is more easily collected than survival data because once nests are located, reproduction measured by fledging rate can be observed directly. Recent advances in tracking and global positioning system transmitter technology may help close knowledge gaps for adult and juvenile survival.

Studies of resource use were the least numerous (16 studies; 30%), perhaps due to the logistical challenges associated with collecting this type of data. The most informative resource use studies involve trapping and tracking individual ravens, but these techniques require a lot of time, equipment, skill, and funds. However, as with survival studies, improved technology should present more opportunities to study raven resource use, selection, and movement associated with important landscape components and demographic effects (Harju et al. 2018).

In addition to unequal attention given to eco-

logical processes, explanatory covariates were also disproportionately investigated among ecological processes. The most common covariates investigated by occurrence studies were vegetation land cover (8 studies; 25%), human settlement and recreation (7 studies; 23%), and linear rights-of-way (7 studies; 23%). Covariates (or strata) of raven occurrence that remain under-studied are: raven age (0 studies), raven sex (0 studies), livestock effects (2 studies; 6%), physiography (1 study; 3%), point subsidies (3 studies; 10%), season (3 studies; 10%), and time of day (2 studies; 6%). Temporal variation in raven occurrence and resource use has not been quantified adequately. Additionally, most studies investigating raven occurrence in relation to vegetation land cover have been carried out in areas where raven densities historically were low but where vegetation land cover has been converted or otherwise disturbed by human activities, meaning that the recent raven occupancy has increased in response to anthropogenic resources and infrastructure beyond simple land cover. In other words, there is a risk of confounded effects between altered land cover and the human enterprise that led to the altered land cover. This problem merits further investigation but has been given serious attention at least once in the literature. O'Neil et al. (2018) used Bayesian hierarchical occupancy models to uncouple the relative contributions of these influences on raven occurrence. Spatial predictions of raven occurrence were developed for both a natural effects model and an anthropogenic effects model. An anthropogenic influence index was then estimated by calculating the difference between these models. The anthropogenic influence index can then provide managers a spatially explicit tool for identifying appropriate management actions based on the factors influencing local raven numbers.

As with other environmental factors, land cover relationships may not adequately describe raven populations and behavior in other ecoregions of North America. Some authors suggest that region-wide surveys (Boarman 2003, White 2006) would continue to reveal spatial variation in raven occurrence and establish baselines for future monitoring and management actions. This approach might prove to be particularly appropriate for the Mojave Desert and Columbia Plateau, where new energy infrastructure construction is expanding across relatively undisturbed habitats (Boarman 2003).

Similar to occurrence studies, unequal consideration of explanatory covariates characterized resource use studies. This result is not surprising considering resource use studies are costly and often involve marking and following individual ravens. The most common covariates investigated by resource use studies were vegetation land cover (7 studies; 41%), linear rights-of-way (7 studies; 41%), and human settlements (6 studies; 35%). Covariates of raven resource use that remain under-studied (2 or fewer studies) were resource use related to other species (2 studies; 12%), physiography (0 studies), recreation (0 studies), supplemental water (2 studies; 12%), and time of day (2 studies; 12%). As with raven occurrence, temporal variation in resource use patterns generally has not been addressed, but should be. One potential solution to lowering the logistical barriers for future resource use studies would be to focus on raven use of specific resources such as supplemental water (Boarman 2003) in areas where surface water otherwise is limiting in arid ecoregions. Improved technology likely will contribute to future opportunities here as well.

Demography represented the second-most-common ecological process investigated, but the disproportionate focus on raven reproduction (17 studies; 81%) reduces these studies' collective utility. Additionally, 6 of these studies were short communications or notes. The relatively small number of studies (11; 52%) investigating covariates of survival or reproduction represents the biggest shortcoming in the prevailing raven demography literature. As was the case for resource use studies, the most commonly studied covariates of reproduction were human settlements and vegetation land cover. In contrast, only 4 studies reported raven survival (19%). The lack of data on covariates influencing survival and reproduction inhibits understanding raven population dynamics across ecoregions. This lack of data also could limit the reliability of future demographic models, such as those called for by Boarman (2003) to assess the potential effects of future management actions on raven populations. This concern applies strongly to ecoregions where demographic data remain uncollected. Studies

of raven survival are rare because they require the greatest investment in time, effort, training, and funds. Collection of these crucial data awaits future studies of individually marked birds (Kelly et al. 2002).

Management implications

This review highlights important information, limitations, and gaps in raven ecology relevant to management of raven populations. Resource agencies or managers seeking to predict the effects of raven management actions may benefit by first considering if adequate scientific support for proposed actitons exists and by supporting ecological studies designed to fill any significant knowledge gaps. Important aspects of raven ecology likely vary regionally, and we urge caution when applying findings from 1 ecoregion to another ecoregion. For example, raven juvenile survival varies substantially between the Mojave Desert and coastal Washington state, USA. Additional demographic studies involving individually marked birds would increase our understanding of factors related to demographic parameters such as survival, which likely vary across ecoregions, and improve our confidence in the efficacy of future management actions. Morever, additional studies in ecoregions impacted by ravens, but where ravens are relatively unstudied, would increase our understanding of potential geographic variation in raven ecology and increase our ability to prescribe ecoregion-appropriate raven management actions.

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Supplemental material

Supplemental material can be viewed at https://digitalcommons.usu.edu/hwi/vol15/iss3/8.

Literature cited

Baltensperger, A. P., T. C. Mullet, M. S. Schmid, G. R. W. Humphries, L. Kövér, and F. Huettmann. 2013. Seasonal observations and machine-learning-based spatial model predictions for the common raven (*Corvus corax*) in the urban, sub-arctic environment of Fairbanks, Alaska. Polar Biology 36:1587–1599.

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 the Southern California Academy of Sciences 101:86–102.

Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). Pages 1–32 *in* A. F. Poole and F. B. Gills, 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.

Buckland, S. T. , D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, United Kingdom.

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.

Camp, R. J., R. L. Knight, and J. Freilich. 1993. Common raven populations in Joshua Tree National Monument, California. Western Birds 24:198–199.

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(2): 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., K. B. Howe, M. L. Casazza, and D. J. Delehanty. 2014*a*. 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. 2014*b*. 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 243:108409.

Dunk, J. R., R. N. Smith, and S. L. Cain. 1997. Nest-site selection and reproductive success in common ravens. Auk 114:116–120.

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(9): e03257.

Engel, K. A., and L. S. Young. 1992*a*. Movements and habitat use by common ravens from roost sites in southwestern Idaho. Journal of Wildlife Management 56:596–602.

Engel, K. A., and L. S. Young. 1992*b*. Daily and seasonal activity patterns of common ravens in southwestern Idaho. Wilson Bulletin 104:462–471.

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.

Freeman, B. G., and E. T. Miller. 2018. Why do crows attack ravens? The roles of predation threat, resource competition, and social behavior. Auk: Ornithological Advances 135:857–867.

Gaines, W., M. Haggard, J. Begley, J. Lehmkuhl, and A. Lyons. 2010. Short-term effects of thinning and burning restoration treatments on avian community composition, density, and nest survival in the eastern Cascades dry forests, Washington. Forest Science 56:88–99.

Gibson, D., E. J. Blomberg, M. T. Atamian, S. P. Espinosa, and J. S. Sedinger. 2018. Effects of power lines on habitat use and demography of greater sage-grouse (*Centrocercus urophasianus*). Wildlife Monographs 200:1–41.

Groves, C. R., D. B. Jensen, L. L. Valutis, K. H. Redford, M. L. Shaffer, J. M. Scott, J. V. Baumgartner, J. V. Higgins, M. W. Beck, and M. G. Anderson. 2002. Planning for biodiversity conservation: putting conservation science into practice: a seven-step framework for developing regional plans to conserve biological diversity, based upon principles of conservation biology and ecology, is being used extensively by the nature conservancy to identify priority areas for conservation. BioScience 52:499–512.

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(7): 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.

Kelly, J. P., K. L. Etienne, and J. E. Roth. 2005. Factors influencing the nest predatory behaviors of common ravens in heronries. Condor 107:402–415.

Knight, R. L., D. P. Anderson, and N. V. Marr. 1991. Responses of an avian scavenging guild to anglers. Biological Conservation 56:195–205.

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 rights-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.

Knight, R. L., H. A. Knight, and R. J. Camp. 1995. Common ravens and number and type of linear rights-of-way. Biological Conservation 74:65–67.

Kristan, W. B., III, and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology 84:2432–2443.

Kristan, W. B., III, and W. I. Boarman. 2007. Effects of anthropogenic developments on common raven nesting biology in the west Mojave Desert. Ecological Applications 17:1703–1713.

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.

Linton, C. B. 1899. Observations on the American raven in Southern California. Bulletin of the Cooper Ornithological Club 1:68–69.

Linz, G. M., C. E. Knittle, and R. E. Johnson. 1992. Home range of breeding common ravens in coastal southern California. Southwestern Naturalist 37:199–202.

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.

Marzluff, J. M., and B. Heinrich. 1991. Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. Animal Behaviour 42:755–770.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'Amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. Bioscience 51:933–938.

Omernik, J. M. 1995. Ecoregions: a framework for managing ecosystems. The George Wright Forum 12(1):35–50.

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.

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.

Restani, M., J. M. Marzluff, and R. E. Yates. 2001. Effects of anthropogenic food sources on movements, survivorship, and sociality of common ravens in the Arctic. Condor 103:399–404.

Restani, M., and J. S. Lueck. 2020. The emerging conflict of common ravens roosting on electric power transmission line towers in Montana, USA. Human–Wildlife Interactions 14:451–460.

Roth, J. E., J. P. Kelly, W. J. Sydeman, and M. A. Colwell. 2004. Sex differences in space use of breeding common ravens in western Marin County, California. Condor 106:529–539.

Scarpignato, A. L., and T. L. George. 2013. Space use by common ravens in marbled murrelet nesting habitat in northern California. Journal of Field Ornithology 84:147–159.

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.

Sullivan, B. L., E. L. Kershner, S. P. Finn, A. M. Condon, D. M. Cooper, and D. K. Garcelon. 2011. Nest-site characteristics of red-tailed hawks and common ravens on San Clemente Island, California. Journal of Raptor Research 45:252–256.

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.

Webb, W., and N. Ellstrand. 2003. First record of double brooding by the common raven. Western Birds 33:258–261.

White, C. 2005. Hunters ring dinner bell for ravens: experimental evidence of a unique foraging strategy. Ecology 86:1057–1060.

White, C. 2006. Indirect effects of elk harvesting on ravens in Jackson Hole, Wyoming. The Journal of Wildlife Management 70:539–545.

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.

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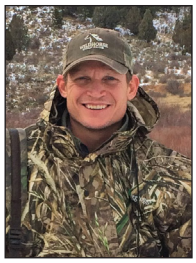

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