

## Synthesis

# Synthesis of nest predation impacts of common ravens on sensitive avian species

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**Abstract:** Decades of mounting scientific evidence have revealed that common raven (*Corvus corax*; raven) population numbers have been increasing across nearly all regions of their geographic range in North America. Concomitantly, numerous native wildlife species have experienced elevated predation rates from ravens as populations have increased and expanded their range. Managers are concerned that increased raven predation of many threatened and endangered avian species in the U.S. and Canada during nesting periods may be hampering species recovery. We explored the literature to aggregate existing knowledge and evaluate the impacts of raven predation on nests and young of sensitive avian species. We used this information to develop a simple relative index for each species, the “Raven Impact Index” (RII). The RII incorporated the species demographic rates, abundance of ravens in relation to each sensitive species’ breeding range, and the degree of overlap between raven and sensitive prey distributions. We also developed a second relative descriptor describing our confidence in each RII, termed a “Impact Credibility Index (ICI).” The species ICI was based on the number of published studies and the type of evidence presented (e.g., circumstantial vs. direct). We found evidence of nest predation on 8 sensitive avian species and suspected nest predation on 1 additional species. All species shared aspects of nesting biology that suggested they would likely be susceptible to raven nest predation. The RII varied among prey species, with greater sage-grouse (*Centrocercus urophasianus*) having the highest relative impact values, followed by snowy plover (*Charadrius nivosus nivosus*), marbled murrelet (*Brachyramphus marmoratus*), and Gunnison sage-grouse (*Centrocercus minimus*). Our species RII is intended to inform management decisions regarding actions that mitigate the negative effects of raven predation of sensitive avian species. Although elevated nest predation may be of high conservation concern, it is important to recognize that all of the sensitive native prey species we established an RII for also face multiple conservation threats.

**Key words:** California condor, *Centrocercus minimus*, *Centrocercus urophasianus*, *Charadrius nivosus nivosus*, common raven, *Corvus corax*, greater sage-grouse, Gunnison sage-grouse, *Gymnogyps californianus*, nest predation, snowy plover

**THE COMMON RAVEN** (*Corvus corax*; raven) has one of the largest natural breeding distributions of any avian species, spanning most of the Holarctic and including distinctly different ecosystems (Boarman and Heinrich 1999). This relatively large distribution encompasses most of Canada and the western United States, northern Europe, Greenland, Iceland, Siberia, south into central China, northern India, and west to northern Africa (Cramp et al. 2014). Ravens

possess several key characteristics that increase the risks they pose to other species, including generalist foraging strategies and high behavioral plasticity (Boarman and Heinrich 1999). Considered omnivorous, ravens forage opportunistically and exploit novel resources (Boarman and Heinrich 1999). They readily expand into landscapes with anthropogenic disturbances, which provide supplemental resources including food, water, nesting substrates, and

hunting perches (Boarman and Heinrich 1999, Hanks et al. 2009, Webb et al. 2011).

The continued expansion of human enterprise across western North America (Leu et al. 2008) likely foreshadows increasing negative impacts of ravens on sensitive species within western ecosystems. As various forms of anthropogenic features (e.g., energy infrastructure) and conversion of land cover types (e.g., agricultural activities) expand in rural environments, raven reproduction and survival rates can increase (Webb et al. 2011), elevating population densities above what they would be in the absence of these resource subsidies (Coates et al. 2020). Elevated subsidies can create or exacerbate a phenomenon known as “hyperpredation,” in which predator numbers decouple from a previous natural carrying capacity due to subsidies, food resource, or other resources (Smith and Quin 1996). Under hyperpredation, predator populations are no longer regulated by declining prey populations and continue to depredate native prey even when rare (Sinclair et al. 1998, Kristan and Boarman 2003). This may be the case with ravens.

Raven populations have grown consistently over the past 53 years in western North America (Harju et al. 2021), and they have done so despite substantial declines in sensitive prey species sympatric with ravens. Avian and other egg-laying species are especially susceptible to predation by ravens because ravens are effective egg predators. Susceptible avian species include some that are currently recognized as sensitive under state or federal listings. For example, ravens are the primary predators of the U.S. federally threatened Agassiz’s desert tortoise (*Gopherus agassizii*) during the first 7–8 years of a tortoise’s life (Boarman 2003; Esque et al. 2010; Berry et al. 2013, 2020). Ravens also likely have important impacts on other species that have not received study or attention. Despite managers’ increased concerns for protecting sensitive avian species, no recent attempts have been made to summarize the growing body of research on the ecological impacts of ravens from a conservation biology perspective.

We reviewed the scientific literature to synthesize the current state of knowledge of impacts of nest predation by ravens on avian species of conservation concern (defined as species that have state and/or federal or provincial

legal protected status within the United States and/or Canada). Because the severity of these impacts varies by species, we developed an index for relative risk of nest predation by ravens. We refer to this index as the “Raven Impact Index” (RII), which integrated: (1) predicted abundance of ravens within each sensitive species’ geographic range; (2) reported evidence negative impact to a demographic rate of the sensitive species; and (3) the geographic range overlap between ravens and each sensitive species’ breeding range. Our goal in generating this metric was to provide managers with a way to gauge the risk that ravens pose to each species.

Variation exists between individual species in the amount of available scientific information. We calculated a descriptor of confidence for the RII associated with each sensitive species, termed the “Impact Credibility Index” (ICI), to account for variation in species-specific scientific information. This ICI incorporated the number and type (e.g., circumstantial vs. direct) of studies reporting evidence of raven depredation on sensitive species. Finally, we evaluated the breeding biology of sensitive species subject to raven depredation to identify traits shared by sensitive species. For example, nest building behavior and/or habitat degradation issues may increase nest visibility and expose species to higher rates of nest depredation by ravens. Our overall goal was to summarize prevailing information of ecological impacts of growing raven populations to help guide comprehensive management strategies currently in development by state and federal agencies within the United States.

## Methods

### Impacts of nest predation on sensitive species

We defined listed avian species as those breeding in the United States and/or Canada and listed as “threatened” or “endangered” at the federal, state, or provincial level, including protected sub-species and distinct population segments. We obtained names of federally listed species under the Endangered Species Act of 1973 (ESA) in the United States published by the U.S. Fish and Wildlife Service (USFWS 2018) and the list of species from Canada Species at Risk Act (SARA) published by the Minister of the Environment and Climate Change



**Figure 1.** Federal, state, or provincially listed “threatened” or “endangered” avian species in the United States and/or Canada impacted by nest predation by common ravens (*Corvus corax*). Top row, greater sage-grouse (*Centrocercus urophasianus*), snowy plover (*Charadrius nivosus nivosus*), and marbled murrelet (*Brachyramphus marmoratus*; photos courtesy of A. Schmierer, G. Lasley, and Audubon Society, respectively). Middle row, greater sandhill crane (*Antigone canadensis tabida*), California condor (*Gymnogyps californianus*), and San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*; photos courtesy of T. Koerner, D. Graham, and T. Ross, respectively). Bottom row, least tern (*Sterna antillarum*), Great Lakes piping plover (*Charadrius melodus circumcinctus*), and Gunnison sage-grouse (*Centrocercus minimus*; photos courtesy of A. Schmidt, Mdf [username], and A. Schmeierer, respectively).

(2018). State and/or provincially listed threatened or endangered species were identified by reviewing U.S. state and Canadian provincial government lists published online. We excluded listed species whose distributions were not sympatric with ravens as determined using geographic range maps published in *The Birds of North America* (Rodewald 2018) and sighting data published on eBird (Sullivan et al. 2009).

In 2020, we searched the published scientific literature to locate all primary sources of evidence of nest predation impacts by ravens on each of the listed species identified in the previous step. As a starting point, we reviewed species accounts in *The Birds of North America* (Rodewald 2018). We searched each species account, including the cited literature for infor-

mation related to nest predation by ravens and references to pursue in the primary literature. We also used the search engine Google Scholar with the search term “raven” combined with each sensitive species’ common English name, as such: “[species name] raven.”

We used primary sources, including peer-reviewed scientific literature and government documents, to assign each taxon to a raven impact category, either (1) known impacted or (2) unknown if impacted. We included species in the impacted category if at least 1 primary source included direct or indirect evidence of nest predation by ravens or described direct management to address nest predation by ravens.

After identifying the impacted species (Figure 1), our goal was to develop a simple rela-



tive descriptor that compiled information about potential impacts within the sensitive species geographical range. The index RII was 1, 2, or 3 from low to high impact, respectively. The first metric predicted a raven abundance index within each sensitive species' geographic range during 2018 using Breeding Bird Survey data (BBS; Sauer et al. 2017), as described in Harju et al. (2021). We assigned the predicted abundances across sensitive avian species into 1 of 3 categories (low, medium, and high) using a score value of 1 (0–3.3 ravens per survey), 2 (3.4–6.6 ravens), or 3 ( $\geq 6$  ravens), respectively.

The second metric consisted of the percent of breeding range of a sensitive species that overlapped the geographic range of ravens, calculated in ArcMap 10.4.1 (Environmental Systems Research Institute, Redlands, California, USA) using range data from BirdLife International (2019). BirdLife International range data of ravens was supplemented with data on raven occurrence on BBS routes. We express the proportion of sensitive species breeding range occupied by ravens as a percent. We assigned a value of 1 ( $>0$ –33% overlap), 2 ( $>33$ –66% overlap), or 3 ( $>66$ –100% overlap) to each sensitive species.

The third metric consisted of demographic impacts of nest predation by ravens based on relevant reporting in the literature (see individual species in Results). We categorized the evidence of predation effect having adverse impacts on demographic rates with a 1 (low), 2 (medium), or 3 (high).

Because scoring the descriptive evidence from the literature involved unavoidable subjectivity, we established rules for categorizing evidence. If raven predation was reported as an observation rather than estimated from samples across a population, then we scored this metric as “low.” Also, if the impact was estimated but showed relatively weak evidence (i.e., small biological effect size), then it was also scored as low. Documented impacts of nest predation on nest survival rates at the population level with marginal evidence were scored as “medium.” Evidence of a strong impact (i.e., large biological effect size) on population growth rate was scored as “high.” We then calculated the RII as the product of these 3 metrics (i.e., abundance, geographic range overlap, and demographic impacts).

The RII accounted for the likely interaction between the effects of raven predation on de-

mographic rates of sensitive species with metrics of raven abundance and degree of overlapping geographic range. For example, the impacts of predation will be multiplicatively greater for sensitive species that experience relatively greater abundances of ravens and are relatively more likely to be exposed to ravens across their range. We then divided the multiplicative score for each sensitive species by the maximum possible value (i.e., 27) to provide a normalized index scored of 0–1. Possible scores were not evenly distributed, and thus this normalization reflected accumulation of evidence as scores increased.

We developed 2 additional metrics to evaluate the credibility (ICI) of the RII by ravens for each individual species. The ICI was a simple relative descriptor such that a higher value indicated greater credibility that the available evidence was in fact representing a true raven impact on a sensitive species and was quantified as the number of published studies reporting nest predation by ravens and the quality of evidence reported in the literature. The first metric of the ICI was based on the number of studies where we identified evidence of raven predation on each sensitive species. We considered this a minimum number because it was possible that studies went undetected during our search procedure, although we sought to include all published information. The number of studies may also represent research bias among taxa, such that some species often receive more research attention than others. However, this was an appropriate metric for ICI because consistency in findings among studies provide verification of reported impacts. Our score consisted of 1 (low = 1–2 studies), 2 (3–4 studies), or 3 ( $\geq 5$  studies). For the second metric forming the ICI, we assessed the quality of evidence across studies for each species. We assigned a score of: 0 when predation evidence was absent; 1 when 1 or more observations were made during a direct management action rather during a directed study; 2 when circumstantial evidence of nest predation was presented during a study; or 3 when direct evidence of nest predation was reported as a result of the study. The ICI was calculated as a sum of these 2 metrics and divided by the maximum value to provide a normalized index from 0–1. For ICI, we deemed summation appropriate to allow for equal weighting

**Table 1.** Avian species listed in the United States and Canada impacted by nest predation due to common ravens (*Corvus corax*). U.S. and Canadian federal abbreviations: Ex = extirpated; E = endangered; T = threatened; NL = not listed. States' conservation rankings: S2 = sensitive species rangewide; S3 = vulnerable statewide population; S3B = sensitive species regionally or statewide. ESA = Endangered Species Act.

Common name	Geographic scope of protection (endangered or threatened)	Range of protected populations	U.S. ESA (Year listed)	U.S. states	COSEWIC / SARA <sup>a</sup>
Greater sandhill crane	Central Valley population	British Columbia, Canada; Washington, Oregon, California, Nevada, USA	NL	E (Washington); T (California); S3B (Idaho, USA); SC (Colorado, USA)	NL
Piping plover	Great Lakes distinct population segment	Western Great Lakes, USA; Ontario, Canada	E / T <sup>b</sup> (1985)	NL	E
Snowy plover	Pacific coast distinct population segment	Coastal Washington, Oregon, California	T <sup>c</sup> (1993)	E (Washington); T (Oregon); SC (Colorado)	NL
Least tern	California and interior populations	U.S. Pacific coast; Mississippi River and tributaries; Texas, Montana, Colorado, New Mexico, USA	E (1970)	E (California, Oregon)	NL
Marbled murrelet	California, Oregon, Washington; British Columbia	Coastal British Columbia; Washington, Oregon, California	T <sup>d</sup> (1992)	E (California, Washington); T (Oregon)	T (British Columbia)
California condor	California, Arizona, Utah, USA; Mexico	California, Arizona, Utah	E/T <sup>e</sup> (1967)	E (California)	NL
Greater sage-grouse	Canada; Washington	Alberta, Saskatchewan, Canada; California, Oregon, Nevada, Utah, Washington, Idaho, Colorado, Utah, Montana, Wyoming, South Dakota, USA	NL	T (Washington); S2 (Idaho); S3 (Nevada); SC (Colorado, Utah)	E (Alberta, Saskatchewan); Ex (British Columbia)
Gunnison sage-grouse	Wherever encountered	Colorado, Utah	T (2014)	SC (Colorado); T (Utah)	NL
San Clemente loggerhead shrike	San Clemente Island, California	San Clemente Island, California	E (1977)	NL	NL

<sup>a</sup> Committee on the Status of Endangered Wildlife in Canada/Canada Species at Risk Act

<sup>b</sup> Endangered in Great Lakes Watershed and threatened elsewhere

<sup>c</sup> Populations within 50 miles of the U.S. coast are listed as threatened

<sup>d</sup> Threatened in California, Oregon, and Washington, USA

<sup>e</sup> Endangered except in experimental populations located in Arizona, Nevada, and Utah, USA

of score levels within each metric. Although the ICI was on a relative scale similar to RII, because of fundamental differences in calculation (i.e., summation of 2 values vs. the product of 3 values) we should expect relatively larger values for ICI than RII.

Lastly, we summarized key aspects of each impacted sensitive species' life history. The goals of our life history summaries were to describe the potential severity of raven impacts and identify species-specific factors associated with raven impacts. In this process, we also sought to compare the threat posed by raven predation to other conservation threats faced by each impacted sensitive species as well as to compare the level of raven impacts between species. In particular, we considered life-history traits, nest visual appearance, habitat use, food habits, range, systematics, population trends, other threats or limiting factors, dispersal, vital rates, demography, regulatory protection, predation, and relative impacts of ravens.

## Results

We identified 78 avian species sympatric with ravens that also were listed at the federal level in the United States and/or Canada. We found no evidence for nest predation by ravens for 70 of those species (90%; Appendix 1). We did not quantify to what extent nest predation had been studied for each of those species.

The primary literature yielded evidence of nest predation impacts by ravens for 7 federally listed species (9%). Species with evidence and national listings were piping plovers (*Charadrius melodus circumcinctus*), snowy plovers (*C. nivosus nivosus*), least terns (*Sterna antillarum*), marbled murrelets (*Brachyramphus marmoratus*; murrelets), California condors (*Gymnogyps californianus*), greater sage-grouse (*Centrocercus urophasianus*), and San Clemente loggerhead shrikes (*Lanius ludovicianus mearnsi*; Table 1). Despite a lack of evidence of raven nest predation, we chose to include Gunnison sage-grouse (*C. minimus*), a federally listed species, in our review. We categorized this species as likely impacted due to the substantial similarity in life-history with greater sage-grouse. Greater sage-grouse are impacted by ravens, and the Gunnison sage-grouse was only recently recognized as a distinct species and split from greater sage-grouse (Young et al. 2000). We also chose to include the greater

sandhill crane (*Antigone canadensis tabida*) that appeared on a state list as a threatened or endangered avian species, which has evidence of nest predation by ravens.

The geographic distribution of the overlap between the geographic distribution of ravens and the breeding ranges of sensitive species covered much of Canada and the western United States, with the overlap occurring in 29 states, 13 provinces, and 14 of 16 level I, 31 of 51 level II, and 111 of 182 level III ecoregions (Figure 2; Appendix 2). Estimated raven abundance (i.e., number of ravens observed per BBS route; Harju et al. 2021) across the geographic range of sensitive species varied by multiple orders of magnitude, ranging from 0.03 ravens/route for least terns to 10.56 ravens/route for Gunnison sage-grouse (Figure 2; Table 2). Specific to each sensitive species, the proportion of each species' breeding range that overlapped the range of ravens was generally high, at 70–100% for nearly all species (with the exception of least terns, with 2% overlap; Figure 3). Species name, range, and listing status are shown in Table 1.

Raven-impacted species received variable impact scores, reflective of a range of evidence describing impacts (Table 2). The greater sage-grouse generated the highest impact score, and the score was supported by a high credibility index value (RII = 1.00, ICI = 1.00). This contrasted with the piping plover (RII = 0.11, ICI = 0.17), which generated a low impact score and a weak credibility value. Nesting characteristics were similar for most species, with a preponderance of species nesting near water, on the ground, and with minimal nest concealment (Table 3). The literature described a variety of threats to sensitive species' persistence, with habitat loss/degradation (9 of 9 species) and pollution (6 of 9 species) ranked as 2 most commonly listed threats (Appendix 3). Species results ordered by decreasing RII score are summarized herein.

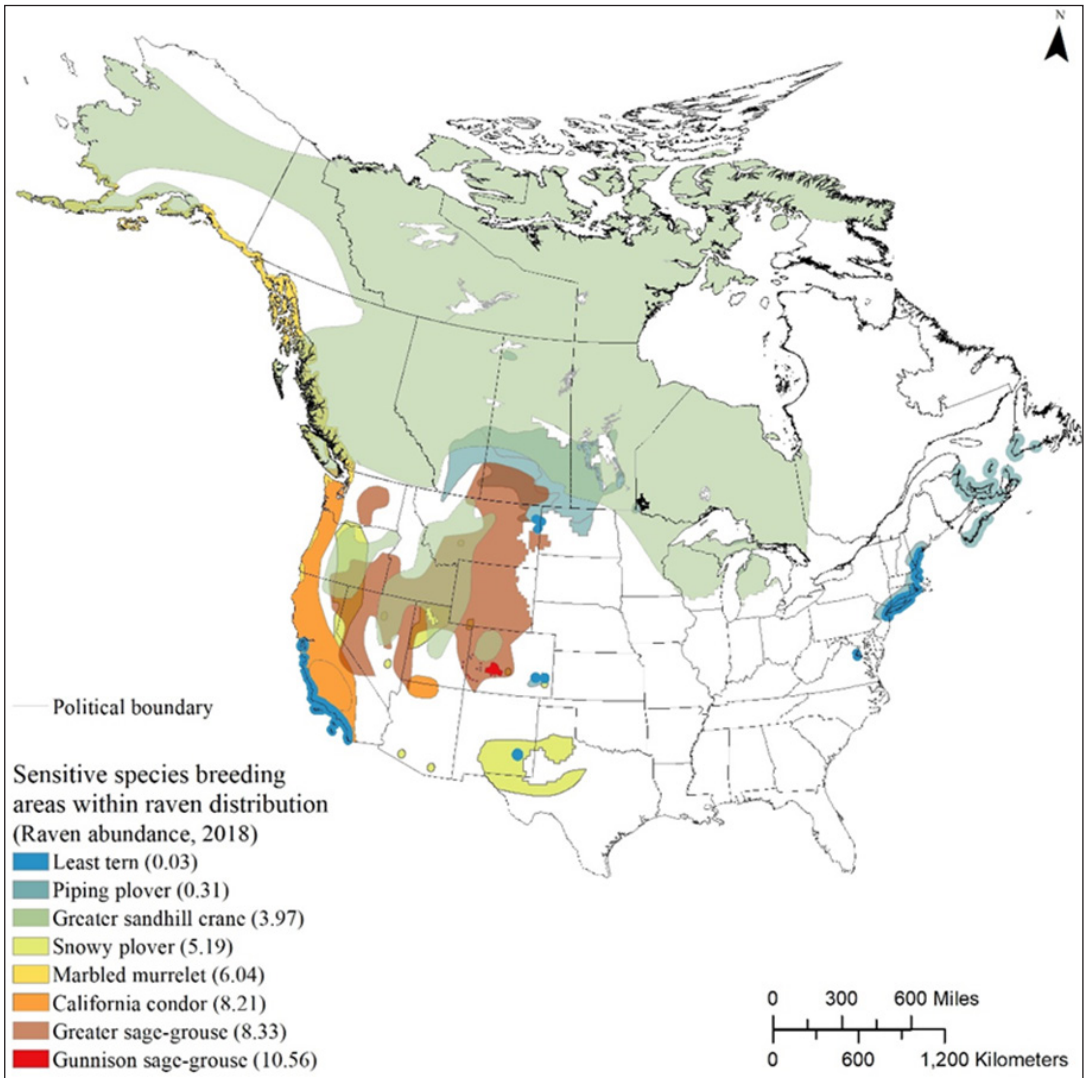
### Greater sage-grouse

Highest protection status: Endangered (Canada SARA)

RII: 1.00

ICI: 1.00

Greater sage-grouse have a lower annual reproductive rate than most North American galliforms (Schroeder 1997, Connelly et al. 2000, Hagen 2011), suggesting that persistent nest



**Figure 2.** Overlap of breeding ranges of sensitive avian species with the geographic range of common ravens (*Corvus corax*; ravens) in the United States and Canada. Sensitive species' breeding range that does not overlap with common ravens or is outside of the United States or Canada not shown. Breeding and geographic ranges obtained from BirdLife International (2019). "Raven abundance, 2018" is the median number of ravens observed per ~40 km Breeding Bird Survey route within each species breeding range (Harju et al. 2021).

predation can have an especially high impact on population growth (Drut et al. 1994, Holloran et al. 2005, Huwer et al. 2008, Taylor et al. 2012). Separately, survival has been associated with population viability, generally (Johnson and Braun 1999), and nest success specifically accounts for the largest variation in greater sage-grouse population growth over time (Taylor et al. 2012).

At large spatial scales, raven presence has long been negatively associated with greater sage-grouse nesting success (Batterson and

Morse 1948, Autenrieth 1981). Recently, research has confirmed that greater sage-grouse avoid areas with ravens during all reproductive stages (Dinkins et al. 2012, 2014) and that raven occurrence near greater sage-grouse nests was negatively associated with nest success (Bui et al. 2010). An increase of 1 observed raven per 10-km transect was associated with an approximately 7.4% increase in the odds of greater sage-grouse nest failure (Coates and Delehanty 2010). Lethal raven removal resulted in an increase in 24-day nest survival rates from 24.8%

**Table 2.** Metrics that were used to develop a common raven (*Corvus corax*; raven) impact index (RII) and impact credible index (ICI) as relative descriptors for state and/or federally listed avian species with evidence of nest predation within the United States or Canada.

Common name	Raven abundance (1–3 points)	Demographic impacts (1–3 points)	% overlap (1–3 points)	RII (0–1) <sup>a</sup>	Studies (1–3 points)	Evidence (1–3 points)	ICI (0–1) <sup>b</sup>
Greater sage-grouse	8.33 (3)	High (3)	92.7 (3)	1.00	10 (3)	Direct (3)	1.00
Snowy plover	5.19 (2)	High (3)	70.2 (3)	0.67	9 (3)	Direct (3)	1.00
Marbled murrelet	6.04 (2)	High (3)	86.6 (3)	0.67	9 (3)	Direct (3)	1.00
Gunnison sage-grouse	10.56 (3)	Medium (2)	100.0 (3)	0.67	0 (0)	Circumstantial (2)	0.33
Greater sandhill crane	3.97 (2)	Medium (2)	98.5 (3)	0.44	5 (3)	Direct (3)	1.00
California condor	8.21 (3)	Low (1)	100.0 (3)	0.33	2 (1)	Direct (3)	0.67
Least tern	0.03 (1)	High (3)	2.0(1)	0.11	4 (2)	Circumstantial (2)	0.67
San Clemente loggerhead shrike	NA <sup>c</sup>	Low (1)	100 (3)	0.33	1 (1)	Circumstantial (2)	0.50
Piping plover	0.31 (1)	Low (1)	71.8 (3)	0.11	0 (0)	Management actions (1)	0.17

<sup>a</sup> RII was calculated as the product of multiple metrics (i.e., “Abundance” (Harju et al. 2021): defined as number of ravens per Breeding Bird Survey route within listed species range; 0.1–3.3 ravens [scored 1], 3.4–6.6 [2], >6.7 [3]; “demographic impacts”: low [1], medium [2], high [3]; and the distributional overlap in range “overlap”: 0–33% [1], 34–66% [2], 67–100% [3]) divided by the maximum value (i.e., 27), to achieve a normalized index of 0–1. RII was developed as a simple relative descriptor of potential risk of sensitive species to elevated predation by ravens across the sensitive species’ breeding range. Because no raven abundance estimates were available for San Clemente loggerhead shrike, RII was calculated as the product of demographic impacts and overlap scores, divided by the maximum possible value.

<sup>b</sup> ICI was calculated as the sum of metrics (i.e., the minimum number of studies reporting raven predation “studies”: 1–3 [scored 1], 4–6 [2], ≥7 [3]; and the strongest type of evidence “evidence”: none [0], management actions [1], circumstantial [2], direct [3]) divided by the maximum value (i.e., 6), to achieve a normalized index of 0–1. ICI was developed as a simple descriptor of the strength of evidence supporting the RII index value.

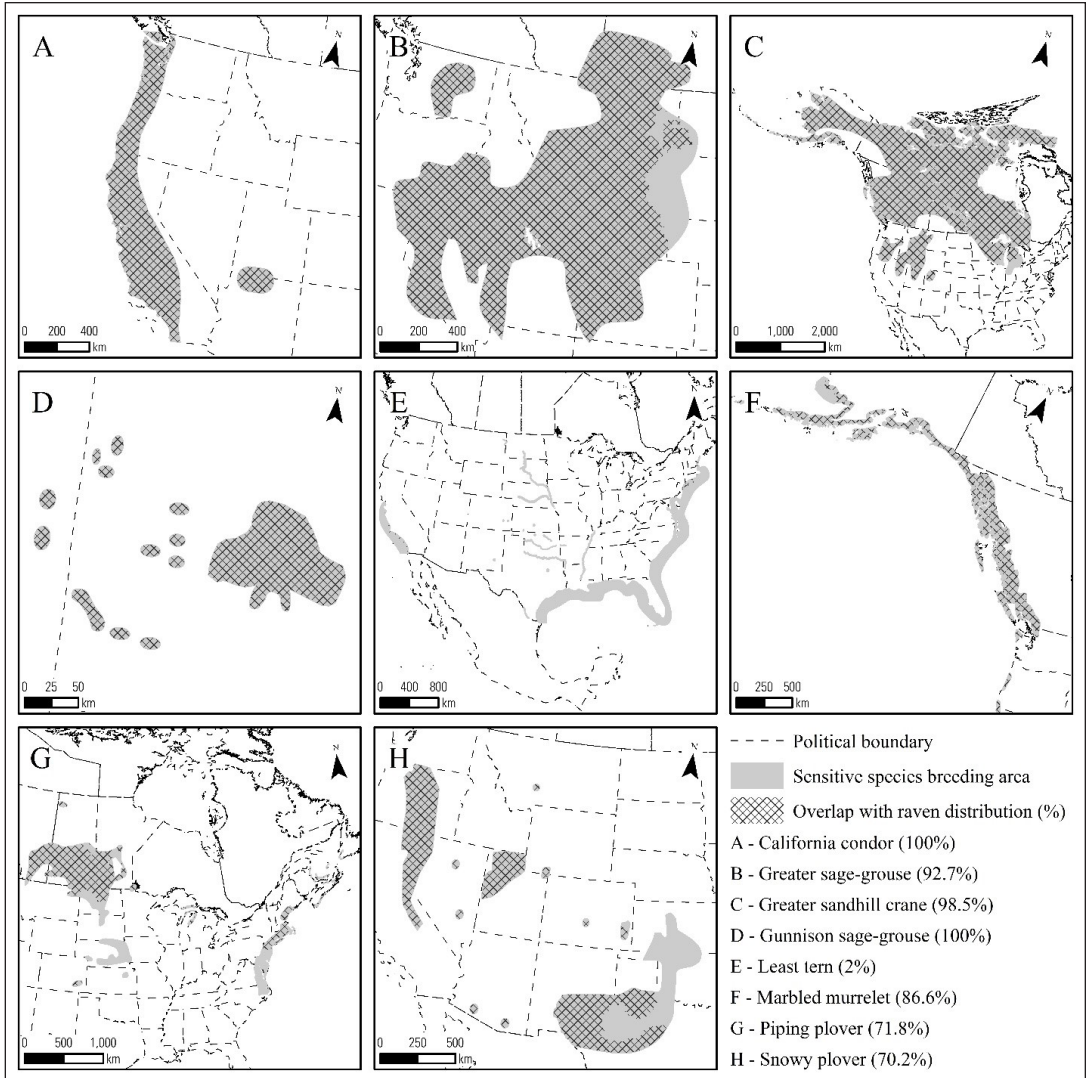
<sup>c</sup> Abundance estimates were based on Breeding Bird Surveys within a listed species range, but due to its small area, no BBS surveys were conducted within the range of San Clemente loggerhead shrike.

to 51.3%, with no change in nest survival in neighboring sites without raven removal (Dinkins et al. 2016).

Several studies report negative associations between higher raven density and greater sage-grouse reproduction. For example, greater sage-grouse nest failure increased in areas with higher raven densities related to a newly developed transmission line (Gibson et al. 2018). Raven im-

pacts on sage-grouse reproduction can be seen at the population level, as male greater sage-grouse counts on breeding leks increased in the year following lethal raven removal (Peebles et al. 2017). Finally, in a recent long-term study by Coates et al. (2020) spanning numerous study sites across the Great Basin, greater sage-grouse nest survival was negatively associated with raven density such that an increase of 1 raven km<sup>2</sup> reduced





**Figure 3.** Full breeding ranges of 8 sensitive species with known or suspected nest predation by common ravens (*Corvus corax*; ravens) and their overlap with the geographic distribution of ravens. Note that breeding range of San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*) is omitted due to extremely restricted range and 100% overlap (San Clemente Island, California, USA). Species ranges outside of the United States or Canada not shown. Range data obtained from BirdLife International (2019).

probability of nest success by ~57%. This study identified an ecological threshold of 0.40 ravens km<sup>-2</sup> where, at this density or greater, ravens were associated with reduced sage-grouse nest survival (Coates et al. 2020), which may reduce overall population size.

The local mechanisms underlying these landscape-level patterns have been directly observed via nest searches and video monitoring. Documented nest predators of greater sage-grouse include mammals, reptiles, and birds, including ravens (Schroeder et al. 1999, Coates

et al. 2008, Bell 2011, Connelly et al. 2011b, Lockyer et al. 2013). One study found that 37 of 87 (42.5%) monitored greater sage-grouse nests were depredated (Coates et al. 2008). Ravens in particular are a major nest predator, accounting for 47% of all nest depredations in Nevada, USA (Lockyer et al. 2013). Video monitoring of nest fate documented ravens depredating 10 out of 17 video-monitored nests in 1 study (Coates et al. 2008) and 3–19% of all monitored nests in 5 separate study areas in Wyoming, USA (Taylor et al. 2017). In a final example, raven-cached

**Table 3.** Nesting characteristics of listed avian species impacted by nest predation from common ravens (*Corvus corax*).

Common name	Nesting habitat	Nest	Nesting habitat structural complexity	Nest spacing	Nest	Nesting substrate
Greater sandhill crane	Seasonal freshwater wetlands	Yes	Simple or none	Low density	Aquatic vegetation	Floating nest
Piping plover	Vegetation-free, broad shorelines	Yes	Simple or none	Semi-colonial	Scrape	Ground
Snowy plover	Vegetation-free, broad shorelines	Yes	Simple or none	Semi-colonial	Scrape	Ground
Least tern	Vegetation-free shorelines	Yes	Simple or none	Colonial	Scrape	Ground
Marbled murrelet	Old-growth coastal coniferous forests	No	Complex	Low density or semi-colonial	None	Tree canopy
California condor	Cliffs, rock outcrops, and large trees	No	Simple or none	Low density	None	Cavities, ledges, caves
Greater sage-grouse	Sagebrush	No	Medium	Low density	Leaves, twigs, feathers	Ground
Gunnison sage-grouse	Sagebrush	No	Medium	Low density	Leaves, bark, grass	Ground
San Clemente loggerhead shrike	Coastal scrub	No	Medium	Low density	Twigs, forbs, bark, feathers, fur	Shrubs

depredated greater sage-grouse eggs were located near 3 raven nests in Idaho, USA (Howe and Coates 2014).

It is likely that other factors, such as habitat loss and/or fragmentation stemming from agriculture, urban expansion, wildfire, conifer expansion, and invasive plants (Schroeder et al. 1999, Crawford et al. 2004, Knick and Connelly 2011, Baruch-Mordo et al. 2013, Coates et al. 2016, Smith et al. 2016, Green et al. 2017, O'Neil et al. 2020) interact with raven densities to have synergistic impacts on greater sage-grouse productivity at large spatial scales. Habitat quality also has been implicated in variation in greater sage-grouse nest success. Studies conducted in altered habitats reported substantially lower

nest success ( $n = 11$ ; mean = 37%; range 12–62%) compared to those conducted in relatively non-altered habitat ( $n = 18$ ; mean = 51%; range 24–71%; Connelly et al. 2011a). As the human footprint increases across large spatial scales (Leu et al. 2008, O'Neil et al. 2018) and raven abundance within the breeding range of greater sage-grouse continues to increase (Harju et al. 2021), the compounding impacts of raven nest predation and other limiting factors are likely to cause further declines in greater sage-grouse populations. Because of the direct evidence of impacts of ravens on greater sage-grouse and their increasing threat as populations expand, we rated the demographic impacts as “high” in the RII.

## Snowy plover

Highest protection status: Threatened (U.S. ESA; Pacific Coast Distinct Population Segment)

RII: 0.67

ICI: 1.00

Snowy plovers are considered one of the least abundant but most studied shorebirds (Jackson et al. 2020). The USFWS has listed the Pacific coast population of snowy plovers as threatened (Page et al. 2009). Snowy plover reproductive success is often low due to predation of eggs and chicks (Neuman et al. 2004, Colwell et al. 2010, Demers and Robinson-Nilsen 2012). This has resulted in several populations of snowy plovers, especially the Pacific coast population, consistently reproducing at levels lower than the number thought necessary for population stability (Colwell et al. 2017) and has been identified as perhaps the most significant factor limiting snowy plover reproduction and slowing recovery of snowy plovers along the Pacific coast (USFWS 2007).

Predation accounted for most nest failures in a study from 1994 to 1997 (Powell et al. 2002), and another reported nest depredation rates of 30–69% of snowy plover nests (Demers and Robinson-Nilsen 2012). In northern California, fledging success was <1.0 (the benchmark for population stability; Nur et al. 1999) in 12 of 16 years of reproductive data collected (Colwell et al. 2017). Finally, predation (including unknown causes of reproductive failure) accounted for 72% of failed snowy plover nests (Colwell et al. 2014).

Numerous species, including those that depredate adult snowy plovers, serve as potential predators of snowy plover eggs and/or chicks (Page et al. 1983, Meslow and Wilson-Jacobs 1984, Page et al. 1985, Warriner et al. 1986, Colwell et al. 2005, Demers and Robinson-Nilsen 2012, Finkelstein et al. 2015, Stinson 2015). Despite a relatively long list of documented predators, only a few mammalian and avian species regularly threaten snowy plover eggs and chicks, with the primary avian predators being California gulls (*Larus californicus*), ravens, and American crows (*Corvus brachyrhynchos*; Meslow and Wilson-Jacobs 1984; Colwell et al. 2005; Demers and Robinson-Nilsen 2012; Ellis et al. 2015, 2020).

Multiple studies include ravens in the list of most frequent nest predators of snowy plovers,

including strong evidence of ravens depredating large proportions of snowy plover eggs and chicks. On the Oregon coast, USA, nest predation by corvids is the primary cause of snowy plover nest failure. Ravens or crows have depredated 22 nests compared to 24 nests failing from all other causes (Lauten et al. 2006). In another study, ravens or crows were responsible for 30–68% of all snowy plover nests depredations (Meslow and Wilson-Jacobs 1984). In California, ravens have depredated 67–69% of snowy plover clutches (USFWS 1993). In another study with 14–35% of snowy plover nests being depredated, most cases ( $n = 50$ ) were attributed to ravens (Powell 2001). A raven was 1 of 4 species documented via video cameras depredating snowy plover nests in the San Francisco Bay area of California (Demers and Robinson-Nilsen 2012), although this study did not quantify predator abundance. Historically, ravens were not recorded depredating snowy plover nests in Monterey Bay, California, until 2002 despite extensive monitoring dating to 1983. However, recently, ravens depredated 12, 36, and 21 nests in 3 years (2002, 2007, and 2008, respectively) in the same population (Page et al. 2009). Video monitoring has confirmed that ravens depredated at least 70% of nests that failed in 1 study (Colwell et al. 2009), and fledging success was inversely correlated to raven abundance in another (Burrell and Colwell 2012). After consideration of the limited reproduction and a slow population recovery (USFWS 2007) of snowy plovers coupled with high rates of nest predation (Colwell et al. 2014), we ranked the demographic impacts of ravens as being “high” for populations of snowy plovers.

## Marbled murrelet

Highest protection status: Threatened (U.S. ESA)

RII: 0.67

ICI: 1.00

Cryptic nesting behavior and camouflaged breeding plumage suggest predation strongly influenced the evolution of marbled murrelet breeding biology, as it has for many other avian species. Despite these adaptations, studies of murrelet nesting biology invariably find that murrelets attain extremely low nest success. The majority of active murrelet nests located and monitored by researchers have failed

(McShane et al. 2004, Peery et al. 2004, Hébert and Golightly 2006). The extremely low murrelet nest success suggests that current nest failure levels are probably higher than historical levels (Beissinger and Peery 2007). The cause of most nest failures appears to be nest predation. Moreover, the current low productivity levels preclude successful recovery of the listed populations of murrelets (McShane et al. 2004, USFWS 2009a, Peery and Henry 2010).

Several avian and mammalian species are confirmed or suspected nest predators of murrelets (Marks and Naslund 1994, Hamer and Nelson 1995, Nelson 1997, Bradley and Marzluff 2003, Peery et al. 2004). While locating nests, determining nest fate, and identifying nest predators is extremely challenging for murrelet researchers, observations reported in multiple sources suggest that ravens and other corvid species may be the most-frequent predators of murrelet eggs and chicks (Manley 1992). A meta-analysis of published and unpublished records of nest predation from real and simulated murrelet nests by ravens and other corvid species identified 10 sources and 24 observations of 1 or more predation events. From this sample, ravens were responsible for 18/52 (35%) of predation events where predation was assigned at the species level (W. Webb, Idaho State University, unpublished data). In a study using artificial nests and carried out in the temperate rainforests of Washington's Olympic Peninsula, USA (Marzluff and Neatherlin 2006), ravens were responsible for ~8% depredations <1 km from campgrounds and settlements. Given that successful recovery of murrelet populations has been hindered by low productivity levels (McShane et al. 2004, USFWS 2009a, Peery and Henry 2010) and ravens are a significant predator of murrelet eggs and chicks (Manley 1992), we scored ravens as having a "high" demographic impact to murrelet populations.

### **Gunnison sage-grouse**

Highest protection status: Threatened (U.S. ESA)

RII: 0.67

ICI: 0.33

Few descriptions existed for predation of Gunnison sage-grouse, and most of the relevant information is anecdotal. Nevertheless, researchers suspect that predation serves as the primary cause of mortality for Gunnison sage-

grouse (Young et al. 2015), as it does for the better-studied greater sage-grouse (Hagen 2011, Knick and Connelly 2011). The best available information suggests that nest predation acts as a localized threat across the range of Gunnison sage-grouse (USFWS 2010, 2014). Long-term stability in the number of birds in the Gunnison Basin population indicates that predation is not impacting this population where most individuals of this species reside (USFWS 2010, 2014). However, nest predation does appear to impact the smaller, isolated satellite populations. For example, studies conducted in the San Miguel satellite population show that elevated nest predation rates have resulted in a lack of recruitment (USFWS 2010). The habitat for the San Miguel population is also characterized by greater amounts of human activities, which promote habitat destruction, habitat degradation, and likely increased abundance of synanthropic nest predators, including ravens (Gunnison Sage-grouse Rangewide Steering Committee 2005, USFWS 2014).

Recent raven trend analyses over 53 years indicate that rate of raven population growth in 1 ecoregion has expansion effects on neighboring ecoregions (Harju et al. 2021), and this movement appears to be from west to east. In the Great Basin, west of Gunnison sage-grouse distribution, research has revealed broad scale impacts of ravens on greater sage-grouse nest survival (Coates et al. 2020). Thus, range expansion of ravens eastward portends forthcoming high exposure of Gunnison sage-grouse to raven impacts. To estimate the potential demographic impact of ravens on Gunnison sage-grouse, we weighed the historic long-term stability experienced by Gunnison sage-grouse populations with the current increasing trends and potential threat of ravens within their range (Harju et al. 2021). Given these factors, we ranked the demographic risk as "medium."

### **Greater sandhill crane**

Highest protection status: Endangered (state of Washington) - Threatened (state of California)

RII: 0.44

ICI: 1.00

Although many species depredate greater sandhill crane nests (Gerber et al. 2020), ravens are a frequent predator, most notably in the listed Central Valley population (Littlefield 1976;



Stern et al. 1987; Littlefield 1995*b*, 1999, 2003). As a result of high predation, nest success in the Central Valley population (29–44%; Littlefield 1976, Stern et al. 1987, Littlefield 1995*a*) is often below that reported elsewhere across their range (77–84%) (Drewien 1973, Bennet 1978). However, not all greater sandhill crane nesting biology studies in the Central Valley Population have found evidence of nest predation by ravens (Littlefield and Lindstedt 1992, Ivey and Scheuring 1997). In addition, ravens do not appear to take the highest number of nests relative to other predators. Studies identifying ravens as nest predators invariably found that other species, such as coyotes (*Canis latrans*), took a higher proportion of greater sandhill crane nests (Littlefield 1976; Stern et al. 1987; Littlefield 1995*b*, 2003). In a study of 25 artificial sandhill crane nests in Idaho, ravens were at or near nests 25 times, with 15 of those events resulting in depredation (Austin and Mitchell 2010). They reported that the time for a raven to reconnoiter, approach, and consume an egg averaged 8.4 minutes (range 1–19 minutes), the shortest in as little as 60 seconds (Austin and Mitchell 2010). This represents a much shorter time than has been reported for thick-billed murre (*Uria lomvia*) nests (Gaston et al. 1985) and greater sage-grouse (Coates 2007). The authors conclude that the rapidity with which ravens depredate and the limitations in successfully determining greater sandhill crane nest predators may explain why these depredation events are infrequently documented. Given the negative impacts of low recruitment, nest predations by ravens present a significant threat to already declining populations of greater sandhill cranes. While evidence of raven impacts to greater sandhill cranes are frequently documented (Littlefield 1976; Stern et al. 1987; Littlefield 1995*b*, 1999, 2003), they are limited to a few populations, and we therefore assigned a “medium” demographic impact of ravens on greater sandhill cranes.

### California condor

Highest protection status: Endangered (U.S. ESA)

RII: 0.33

ICI: 0.67

Demographic models indicated the decline in the historic California condor population

occurred primarily due to excessive adult mortality (Meretsky et al. 2000) rather than low productivity. Prior to release of the captive population in 1992, no confirmed predation records existed, and few observations were made of predation attempts on California condors (Snyder and Snyder 2000). Although few natural predation cases or attempted natural predation events were documented for the historic wild California condor population, the available evidence suggests nest predation by ravens may have impacted California condor reproductive success. For example, Snyder et al. (1986) characterized nest predation by ravens of California condor eggs as the “greatest threat to condor nesting success.” They also documented a successful nest predation event by a raven, numerous cases of attempted nest predation by ravens and located California condor eggshell fragments in 3 old raven nests located near California condor nests. In addition, Snyder et al. (1986) described raven predatory behavior toward nesting California condors as persistent and aggressive. Notable examples of raven predatory behavior toward California condors included 1 individual “jabbing under the abdomen of an incubating California condor” and ravens pursuing California condors as they explore potential nesting sites (Snyder et al. 1986).

The impacts of ravens on the released population of California condors appear substantially less than the historical impacts, for reasons that are not clear. Researchers documented only a single loss of a California condor egg to ravens since reintroduction efforts began in 1992 (Mee and Snyder 2007). The unfamiliarity of contemporary resident ravens with the egg-laying habits of California condors represents a possible explanation for the apparent reduced level of nest predation (Mee and Snyder 2007). However, both species’ increased density would likely elevate the risk of nest predation of California condors by ravens in the future, and, given the extremely low current abundance of wild California condors, even a low frequency of nest depredation could have large negative demographic consequences. Despite the potential increase in this threat, we classified the demographic impact of ravens on California condor populations as “low.”

### San Clemente loggerhead shrike

Highest protection status: Endangered (U.S. ESA)

RII: 0.33

ICI: 0.50

Coupled with habitat conversion, native and non-native nest predators threaten the recovery of San Clemente loggerhead shrikes (Scott and Morrison 1990). Although rarely documented, researchers estimate that nest predation accounts for 44–48% of all San Clemente loggerhead shrike nest failures (Yosef 1996, USFWS 2009c) and is considered the most significant cause of annual mortality (USFWS 2009c). The most frequent nest predators include the endemic San Clemente Island fox (*Urocyon littoralis clementae*), while other significant nest predators include feral domestic cats (*Felis silvestris*), black rats (*Rattus rattus*), rock wrens (*Salpinctes obsoletus*), northern mockingbirds (*Mimus polyglottos*), American kestrels (*Falco sparverius*), red-tailed hawks (*Buteo jamaicensis*), barn owls (*Tyto alba*), and ravens (Eggert et al. 2004, Cooper et al. 2005). However, the scientific literature lacks documentation confirming ravens (and most of the suspected nest predators) as actual nest predators of San Clemente loggerhead shrikes. As a result, we classified the threat of ravens to San Clemente loggerhead shrike populations as “low.” However, Cooper et al. (2005) provided the most direct evidence of predation by ravens. They listed ravens as 1 of 3 potential avian predator species (along with rock wrens and northern mockingbirds) based on the presence of ravens in the immediate vicinity of 5 San Clemente loggerhead shrike nests bearing evidence of avian nest predation.

### Least tern

Highest protection status: Endangered (U.S. ESA)

RII: 0.11

ICI: 0.67

Low productivity, primarily due to predation of eggs and chicks, impedes the recovery of populations of the California least tern (*Sterna antillarum brownii*; Frost 2016) and Interior least tern (*S. a. athalassos*; Kirsch and Sidle 1999). For least terns, predation results in direct mortality, nest failure, renesting, and complete colony failure (Massey and Fancher 1989, Koenen et al. 1996). Least tern predation

events are rarely witnessed, and often little or no evidence remains (Frost 2016). However, witnesses have occasionally observed predation events. In California, observers identified 47 different confirmed or suspected predator species of least terns with ravens ranked as one of the most frequently observed of those species (Liebezeit and George 2002, USFWS 2006, Marschalek 2011).

Due in part to the colonial nesting behavior of least terns, actions of a single predator species or a single individual can result in significant impacts to least tern populations over a few days or an entire nesting season (USFWS 2006). In some instances, nest predation by ravens has resulted in large losses of least tern nests (Marschalek 2011). However, the impacts of ravens on California least tern nesting success varies across sites. The greatest impacts from ravens occur at a small number of sites, apparently perpetrated by a small number of “problem” individuals (Liebezeit and George 2002). During 2010, ravens impacted less than half (17 of 41) of California’s nesting locations, yet at the same time removed 60 eggs from 446 nests at a single colony (Marschalek 2011).

The prevalence of raven predation of least terns in California has been increasing since close monitoring of colonies began in the late 1960s (Fancher 1992). Although their impact is spatially variable, raven predation in California has increased steadily since the late 1960s (Fancher 1992), and ravens are now among the dominant least tern predators (Frost 2014, 2016). Avery et al. (1993) reported ravens depredated a large number of least tern eggs in California between 1983 and 1992, although the authors omitted specific quantities of affected nests. During 2010, ravens were responsible for depredating 203 (13%) of the total least tern eggs lost by predators (Marschalek 2011), whereas in 2013 ravens depredated 84 (26%) of the total eggs lost and ranked first in this category (Frost 2014). This prevalence of raven predation and apparent increase in nest depredations has led us to classify the impact of ravens on California least tern populations as “high.”

External factors such as habitat loss (Atkinson and Dood 2006), supplemental food (Zuria and Mellink 2002), human disturbance (Burger 1984), hydrological modifications (Atkinson and Dood 2006), and reduced foraging oppor-

tunities also impact least tern populations and likely interact with predation rates by ravens and other predators. No records were located of predation by ravens for the Interior or Coastal populations of least terns. However, continuing expansion and growth of raven populations foreshadows potential future impacts to these populations of least terns as well.

### Great Lakes piping plover

Highest protection status: Endangered (U.S. ESA, Canada SARA; Great Lakes Distinct Population Segment)

RII: 0.11

ICI: 0.17

The Great Lakes population of piping plovers is small and appears limited by low productivity caused by nest predation and other factors (USFWS 2009b). Although no direct or circumstantial evidence exists that ravens depredate piping plovers, ravens are a significant predator of closely related snowy plovers (Collwell et al. 2009, 2013), which possess similar life-history traits and limiting factors (Appendix 3). In at least 1 instance, managers believed the threat of predation by ravens sufficient enough to include them on the list of species lethally removed to protect nesting piping plovers (Struthers and Ryan 2005). Because of the small population size, any nest predation by ravens would further lower productivity and negatively impact the recovery of the Great Lakes population of piping plovers. However, the general lack of direct and circumstantial evidence has led us to classify the demographic impacts of ravens to be “low” for Great Lakes piping plovers.

## Discussion

We found evidence of nest predation by ravens for 8 of the 79 avian species listed at the state, provincial, and/or national level within the United States and Canada (Tables 1 and 2; Appendix 2) according to research that documented such impacts. We also added Gunnison sage-grouse to our list of species with impacts based on strong ecological similarity to greater sage-grouse. Although we did not find scientific literature documenting impacts on most listed avian taxa, this does not imply that impacts do not or will not exist. From the literature, it is difficult to distinguish the absence of

impacts from unknown impacts. Many species receive little study, and some impacts, like nest depredation, are difficult to observe without concerted effort.

Although the percentage of known impacted species is small, the spatial extent of raven impacts is substantial. Geographic intersections between the range of ravens and the collective breeding ranges of the identified raven-impacted species occur in southwestern Canada and large portions of the United States, primarily west of the Rocky Mountains. This distributional overlap includes portions of 29 states, 13 provinces, and 111 of 182 unique level III ecoregions (Omernik 1987; Figure 2; Appendix 2).

The listed avian species impacted by ravens appear to share several aspects of their nesting biology. One important shared trait may be nest visibility to ravens. Ravens appear to locate prey primarily through visual searching (Powell 2001, Coates and Delehanty 2008, Conover et al. 2010). Sensitive species currently experiencing raven impacts nest near open water with little or no nest-concealing vegetation or they nest on the ground with minimal nest construction (Table 3). Many documented cases of nest predation by ravens are of waterbirds (Montevicchi 1979, Hothem and Hatch 2004, Kelly et al. 2005, Hayward et al. 2015), and 4 of the impacted species (i.e., greater sandhill cranes, piping plovers, snowy plovers, and least terns) nest on open mounds in marshy habitats or on beaches adjacent to water. Five of the impacted species construct simple scrapes or do not construct any nest (i.e., piping plover, snowy plover, least tern, murrelet, and California condor; Table 3), which further increases nest visibility, especially in the absence of concealing vegetation. Together, these characteristics suggest that nest visibility plays a vital role in influencing nest vulnerability to raven predation for many species.

Murrelets were the surprising exception to this, as they nest in well-hidden pockets of old growth canopy (see results section). As was described for snowy plovers and greater sage-grouse, ravens may be utilizing murrelet behaviors to locate nests (Powell 2001, Coates and Delehanty 2008). For example, ravens appear to locate greater sage-grouse nests by cuing on movements of females to and away from nests during their incubation recess (Coates and

Delehanty 2008). Perhaps ravens typically have difficulty finding well-hidden nests that are not located on the ground.

Several key observations have shed light on how ravens use visual cues to locate and depredate nests, whether nests were concealed or not. In southern California, Powell (2001) observed ravens following the tracks of beach-nesting snowy plovers until the ravens narrowed their attention near the snowy plover nests. Video evidence also revealed that after snowy plovers departed their nests, ravens often landed within 1 m of the nest and walked directly to it (Burrell and Colwell 2012). Ravens also may use the presence of nest exclosures (when in use) to locate nests and depredate fledglings. In 2002, a pair of ravens depredated 2 newly hatched fledglings that had recently departed a nest exclosure in northern California (Colwell et al. 2009). In northeastern Nevada, video-monitoring of greater sage-grouse nests revealed that incubating females exhibited a strong bimodal pattern in daily recesses (Coates et al. 2008). The timing of recesses aligned with the occurrences of predation by ravens, thus indicating that ravens likely were cuing into movement of greater sage-grouse to and from their nests (Coates et al. 2008).

The size of a species' geographic range appears unrelated to vulnerability to nest predation by ravens. This is unsurprising, as raven populations are prevalent throughout the majority of these breeding ranges, and ravens opportunistically select local food sources. One third of the impacted species have relatively small breeding ranges and occur in 1 or 2 ecoregions (i.e., San Clemente loggerhead shrike, Gunnison sage-grouse, and Great Lakes population of piping plovers), while the other species have large ranges spanning 3 or more ecoregions encompassing several states and/or provinces (Appendix 2). Furthermore, family-level taxonomic affiliation appears mostly unrelated to vulnerability to nest predation by ravens. The impacted species group into 7 taxonomic families, including 1 tern (*Laridae*), a murrelet (*Alcidae*), a crane (*Gruidae*), a vulture (*Cathartidae*), and a shrike (*Laniidae*). However, the 2 closely related plover species (*Charadriidae*) and 2 closely related grouse species (*Phasianidae*) each may share traits that make them mutually vulnerable to ravens.

Generating RII and ICI values highlighted deficiencies in our current understanding of raven impacts and the vulnerability of species of conservation concern. For many reasons, the literature was not evenly balanced among species. Each RII value reflected a combination of the relative biological magnitude of raven predation while the ICI provided information on the relative extent of existing scientific knowledge.

Importantly, our indices were inherently influenced by the overall number of studies for each species. For example, a single study presented circumstantial evidence for nest predation by ravens on San Clemente loggerhead shrike, leading to a low RII. Because this species is restricted to a single island, the potential impacts of raven predation are possibly much larger than the impact score derived from existing evidence in the literature. Given that ravens are known predators of mainland loggerhead shrike nests (Poole 1992, Humple and Holmes 2006), their potential threat to the San Clemente loggerhead shrike population may be higher than the current RII suggests. A much higher RII would be warranted if ravens frequently depredate shrike nests, but additional information is lacking.

Each raven-impacted species faces multiple conservation threats, and the relative importance and interactions of various threats, including nest predation by ravens, is unclear. Nevertheless, historical and/or continuing habitat loss and degradation arguably pose the most significant challenges and threaten each species on the impacted list (Appendix 3). Additional threats facing a third or more of the species include pollution (67%), non-native plants (44%), pesticides/herbicides (33%), excessive livestock grazing (33%) and reduced prey/foraging opportunities (33%).

Evaluating the relative impact of nest predation by ravens compared to these threats becomes challenging in the absence of information regarding each threat's pervasiveness and/or the relative demographic impacts of the different threats for each species. Moreover, nest predation likely interacts with other threats. For example, predation rates may be greatly influenced by landscape structure and complexity (Schneider 2001). Therefore, disturbances to landscapes adversely impact quality of habitat



(e.g., fragmentation) and likely increase the efficiency of ravens and other generalist predators in locating their prey. A loss in complexity of habitat that serves as concealment for prey may increase per capita consumption rate by predators (i.e., increase in functional predator–prey response; Redpath and Thirgood 1999). This can be especially problematic for prey species experiencing hyperpredation by generalists that are growing in population size as a result of anthropogenic resource subsidies. Thus, increasing numbers of ravens coupled with reduction of habitat complexity that provides concealment of sensitive prey nests likely has profound impacts on population persistence of these sensitive species.

### Management implications

We have synthesized published scientific studies of raven predation on federal-, state-, or province-listed avian species across multiple ecoregions in the United States and Canada to create a novel, yet simple, empirically based raven impact index for each sensitive species with a corresponding credibility index. These metrics and syntheses of findings from scientific papers may serve as informational support for wildlife biologists and administrators to help guide management decisions aimed at reducing the impacts of raven populations on sensitive prey species. However, human-subsidized, expanding raven populations likely impact a greater range of species (and communities) than those with protection status identified here. For example, studies have identified substantial impacts of nest predation by ravens on black-crowned night heron (*Nycticorax nycticorax*), an unprotected species, on Alcatraz Island, California (Brussee et al. 2016, Brussee and Coates 2018). Thus, ravens may have even larger impacts on more abundant species given raven's generalist omnivorous diet (e.g., Kristan et al. 2004). Not only have we documented impacts or likely impacts of ravens on 9 sensitive avian species, recent research has documented dramatic population growth and range expansions of ravens (Harju et al. 2021). To better conserve these sensitive avian species, other non-avian sensitive species (e.g., Agassiz's desert tortoise), and other wildlife populations in general, the broader impacts of ravens on ecosystems merit further investigation.

### Acknowledgments

The authors would like to thank P. Jackson and S. Espinosa from the Nevada Department of Wildlife for support of this effort. We thank S. Frey (Utah State University), L. Peebles (Wildlife Services), and S. Webster and S. O'Neil (U.S. Geological Survey) for their constructive feedback at various stages of this synthesis. We also appreciate the discussion of various aspects and results of this synthesis with members of an inter-agency Raven Core Team established by the U.S. Fish and Wildlife Service. We thank T. A. Messmer and an anonymous reviewer whose comments enriched the manuscript.

### Supplemental material

Supplemental material can be viewed at <https://digitalcommons.usu.edu/hwi/vol15/iss3/11>.

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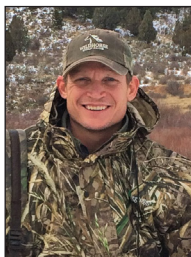
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