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Research Article

Reptiles Under the Conservation Umbrella of the Greater Sage-Grouse

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ABSTRACT In conservation paradigms, management actions for umbrella species also benefit co-occurring species because of overlapping ranges and similar habitat associations. The greater sage-grouse (*Centrocercus urophasianus*) is an umbrella species because it occurs across vast sagebrush ecosystems of western North America and is the recipient of extensive habitat conservation and restoration efforts that might benefit sympatric species. Biologists' understanding of how non-target species might benefit from sage-grouse conservation is, however, limited. Reptiles, in particular, are of interest in this regard because of their relatively high diversity in shrublands and grasslands where sage-grouse are found. Using spatial overlap of species distributions, land cover similarity statistics, and a literature review, we quantified which reptile species may benefit from the protection of intact sage-grouse habitat and which may be affected by recent (since about 1990) habitat restoration actions targeting sage-grouse. Of 190 reptile species in the United States and Canadian provinces where greater sage-grouse occur, 70 (37%) occur within the range of the bird. Of these 70 species, about a third (11 snake and 11 lizard species) have >10% of their distribution area within the sage-grouse range. Land cover similarity indices revealed that 14 of the 22 species (8 snake and 6 lizard species) had relatively similar land cover associations to those of sage-grouse, suggesting greater potential to be protected under the sage-grouse conservation umbrella and greater potential to be affected, either positively or negatively, by habitat management actions intended for sage-grouse. Conversely, the remaining 8 species are less likely to be protected because of less overlap with sage-grouse habitat and thus uncertain effects of sage-grouse habitat management actions. Our analyses of treatment databases indicated that from 1990 to 2014 there were at least 6,400 treatments implemented on public land that covered approximately 4 million ha within the range of the sage-grouse and, of that, >1.5 million ha were intended to at least partially benefit sage-grouse. Whereas our results suggest that conservation of intact sagebrush vegetation communities could benefit ≥14 reptiles, a greater number than previously estimated, additional research on each species' response to habitat restoration actions is needed to assess broader claims of multi-taxa benefits when it comes to manipulative sage-grouse habitat management. Published 2020. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Centrocercus urophasianus*, land treatment, rangelands, sagebrush, Squamata, umbrella species.

Single-species management influences many wildlife conservation efforts in the United States (Simberloff 1998, Evans et al. 2016, Johnson et al. 2017). In an era of ecosystem- and landscape-level resource management, however, managers commonly assume that species-specific habitat protection and management actions also indirectly benefit other wildlife species. This umbrella species concept (Wilcox 1984) infers that many co-occurring species will be protected by conserving the habitat of a single species (Caro and O'Doherty 1999, Roberge and Angelstam 2004). Applying this conservation concept in practice requires that ≥3 criteria are met. First, protecting intact habitat for the umbrella species should benefit the co-occurring species. Second, the range of the umbrella species should be large compared to the range of co-occurring species (Wilcox 1984). Third, restoration or management actions targeting the umbrella species should also benefit, or at least not negatively affect, co-occurring species (Ozaki et al. 2006). Although the umbrella species concept has been criticized as overly simplistic and optimistic (Andelman and Fagan 2000, Cushman et al. 2010, Runge et al. 2019), researchers suggest that species richness of co-occurring (i.e., potential beneficiary) species can be higher in locations where umbrella species are present (Branton and Richardson 2011).

The greater sage-grouse (*Centrocercus urophasianus*) is an important umbrella species in sagebrush vegetation communities

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of western North America, ostensibly benefiting a wide range of taxa (Rowland et al. 2006, Hanser and Knick 2011). This ground-nesting bird occurs in parts of 11 states in the United States and 2 Canadian provinces (Knick and Connelly 2011). Many individuals migrate seasonally across large (4–615 km^2) landscapes to access requisite nesting, foraging, and sheltering habitats (Connelly et al. 2011). The overlap of the sage-grouse distribution with private and government-administered grazing lands, agricultural lands, and lands rich in mineral and energy resources has created conservation conflict and opportunity. Partnerships from local to national levels have formed over the last 2 decades to stem the decline of sage-grouse populations by identifying and protecting the best remaining habitat, restoring degraded areas, and rehabilitating habitat altered by wildfire, oil and gas development, and other disturbances (Belton and Jackson-Smith 2010, Murphy et al. 2013, Duvall et al. 2017).

Since the first petition to federally list the greater sage-grouse under the United States Endangered Species Act (ESA) in 2002, several range-wide habitat conservation strategies have been developed and their implementation is ongoing (U.S. Fish and Wildlife Service [USFWS] 2013). For example, in the last 2 decades, vegetation on >2 million ha of private land has been actively managed under the guidance of the Greater Sage-Grouse Comprehensive Conservation Strategy (Stiver et al. 2006) and Sage-Grouse Initiative (U.S. Department of Agriculture 2015). On public lands, the United States Department of Interior Bureau of Land Management (BLM) and United States Department of Agriculture Forest Service (USFS) Resource Management Plans have recommended management actions across millions of hectares, including the removal of single leaf-pinyon pine (*Pinus monophyla*), Colorado pinyon (*P. edulis*), western juniper (*Juniperus occidentalis*), and Utah juniper (*J. osteosperma*) woodlands, control of cheatgrass (*Bromus tectorum*) and other exotic annual grasses, and restoration of big sagebrush (*Artemisia tridentata*) following wildfires. Given the recent emphasis being placed on protecting intact sage-grouse habitat and the extent of management actions where sagebrush has been lost or degraded (Arkle et al. 2014), there is growing interest among stakeholders in assessing potential benefits or consequences of these expansive conservation efforts on co-occurring species. The Sagebrush Science Initiative sponsored by the Western Association of Fish and Wildlife Agencies and the USFWS is a good example (https://www.wafwa.org/initiatives/sagebrush_ecosystem_initiative/, accessed 18 Sep 2019).

There is limited information concerning potential benefits to different wildlife species under the sage-grouse conservation umbrella, which is worrisome given that a one-size-fit-all approach rarely works in wildlife habitat management (Zipkin et al. 2010). A few studies have addressed this issue, mainly focusing on other birds and mammals (McAdoo et al. 2004, Beck et al. 2012, Copeland et al. 2014, Donnelly et al. 2017, Carlisle et al. 2018*a*). Information on reptiles is particularly scarce, especially regarding the potential responses of reptile taxa to restoration actions. A few recent studies, however, have included reptiles in their assessments of the likelihood of protecting wildlife species under the sage-grouse umbrella (Rowland et al. 2006, Carlisle et al. 2018*b*, Runge et al. 2019). These assessments focused solely on species considered to be sagebrush obligates or associates. Collectively, these studies examined only 24 reptile species, including 9 species in the Great Basin (Rowland et al. 2006), 13 species in Wyoming, USA (Carlisle et al. 2018*b*), and 8 species across the range of the greater sage-grouse (Runge et al. 2019). But only 5 lizard species were common between Rowland et al. (2006) and Runge et al. (2019) and only 1 snake species was common between Carlisle et al. (2018*b*) and Runge et al. (2019).

Because of the lack of consistency among these assessments and the likely need for information on reptile species beyond those considered sagebrush obligate or sagebrush associate, we sought to conduct a more comprehensive and quantitative assessment of which western North American reptile species may benefit from sage-grouse conservation efforts, namely conservation of intact sage-grouse habitat and restoration of degraded areas. Our specific objectives were to determine which reptile species are likely to benefit most from protecting intact sage-grouse habitat, how likely are restoration treatments targeting sage-grouse to overlap with each reptile species, how likely are these management actions to alter a substantial portion of each species' range, what is the prevalence of different sage-grouse treatment actions between 1990 and 2014, and how might different reptile species be affected by these various treatments according to past studies and relative to their conservation status.

STUDY AREA

This study spanned the range of the greater sage-grouse as estimated in 2014 (Lindstrom 2014), which included 70 million ha across western North America in California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, South Dakota, Utah, Washington, and Wyoming, USA, and in Alberta and Saskatchewan, Canada (Fig. 1). The vast range of the sage-grouse encompassed many environmental gradients and land cover types (West and Young 2000, Shinneman 2019), but the birds were generally associated with sagebrush-steppe and sagebrush semi-desert plant assemblages (Crawford et al. 2004). The sage-grouse range had a mean elevation of 1,602 m (range = 129–4,096 m), mean annual precipitation of 334 mm (range = 122–1,311 mm), and mean annual temperature of 6.9°C (range = −3.1–14.3°C; 30-year average 1981–2010; Parameter-elevation Relationships on Independent Slopes Model [PRISM] Climate Group, Oregon State University, http://prism.oregonstate.edu, accessed 17 Sep 2019).

METHODS

We first identified all reptile species that occur in the 11 states and 2 provinces in the greater sage-grouse range by examining reptile range maps that follow standard taxonomy and nomenclature (Crother 2017). Range maps

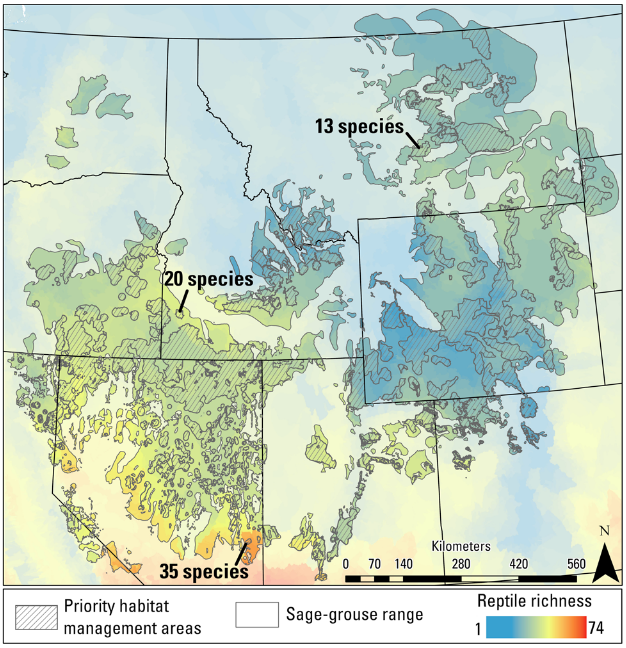

Figure 1. Reptile species richness created from compiling individual range polygons in western North America, 2008–2016. Large polygons depict the range of the greater sage-grouse in 2014 and polygons nested within these show priority habitat management areas designated for greater sage-grouse. Numbers indicate reptile species richness estimated for particular locations, as examples.

are defined as the extent of a species' geographic limits (U.S. Geological Survey [USGS] 2018). We then used a geographic information system (GIS; Esri ArcGIS 10.6, Redlands, CA, USA) to determine the overlap between the range of each reptile species (USGS 2018, International Union for the Conservation of Nature [IUCN] 2017) and the 2014 range of the greater sage-grouse (Lindstrom 2014) buffered by 35 km. The 35-km buffer distance represents the maximum distance the habitat management areas polygon (BLM 2017) extends beyond the sage-grouse range polygon (Lindstrom 2014). We also used the species' range maps to depict reptile species richness across the range of the greater sage-grouse (Fig. 1). Gap analysis project range maps were unavailable for 11 of the 190 reptile species within the study area (USGS 2018), so we used other sources (Leache 2009, Krysko et al. 2017, Nafis 2018) for the 11 species: forest sharp-tailed snake (*Contia longicauda*), panamint rattlesnake (*Crotalus stephensi*), California kingsnake (*Lampropeltis californiae*), speckled kingsnake (*Lampropeltis holbrooki*), Madrean mountain kingsnake (*Lampropeltis knoblochi*), desert kingsnake (*Lampropeltis splendida*), rosy boa (*Lichanura orcutti*), prairie lizard (*Sceloporus consobrinus*), southwestern fence lizard (*Sceloporus cowlesi*), Sonoran lyresnake (*Trimorphodon lambda*), and California lyresnake (*Trimorphodon lyrophanes*). We did not include 8 of these species in analyses because they did not overlap with the range of the sage-grouse: forest sharp-tailed snake, speckled kingsnake, Madrean mountain kingsnake, desert kingsnake, rosy boa, southwestern fence lizard, Sonoran lyresnake, and California lyresnake. We did not include 3 of these species because GAP predicted habitat maps were unavailable: panamint rattlesnake, California kingsnake, and prairie lizard.

To determine which reptile species might benefit most from protection of intact sage-grouse habitat, we refined our list of relevant reptile species by assessing the similarity of each species' habitat to habitats occupied by sage-grouse. Using reclassified (Table S1, available online in Supporting Information) land cover data derived from LANDFIRE (2014), we calculated the proportion of each land cover type across the predicted habitat of each species (USGS 2018). The GAP predicted habitat maps are described as:

> "Mapped areas represent places where the environment is suitable for the species to occur (i.e., suitable to support one or more life history requirements for breeding, resting, or foraging), while areas not included in the map are those predicted to be unsuitable for the species. These habitat maps are created by applying a deductive habitat model to remotely-sensed data layers within a species' range. The deductive habitat models are built by compiling information on species' habitat associations into a relational database. Information is compiled from the best available characterizations of species' habitat, which included species accounts in books and databases, as well as primary peer-reviewed literature" (https://www.usgs.gov/core-science-systems/science-analytics-and-synthesis/gap/science/species-data-overview, accessed 18 Sep 2019).

We used these predicted habitat maps as a proxy for species distributions, which provided a finer resolution and ecologically more realistic potential area of occupancy compared with range maps. The predicted habitat maps for each reptile was based on information compiled and modeled from 2008 to 2016 in the western United States, which restricted subsequent analyses to the United States (USGS 2018).

For each reptile species, we calculated a Bray-Curtis dissimilarity (or distance) value (Ricotta and Podani 2017) by comparing the land cover proportions of the sage-grouse to those of the reptile. We focused on reptiles with dissimilarity values <0.5 (group I species), whereas we classified reptiles with values >0.5 (group II species) as relatively dissimilar to sage-grouse with regards to land cover (i.e., a component of habitat) within their distribution. We selected this cutoff because it was a natural breakpoint in the data and because it conveniently divided the reptiles into 2 similarly sized groups. We plotted each species' land cover dissimilarity value and distribution overlap with sage-grouse to rank their potential as a beneficiary species based on both criteria.

To identify which species are potentially influenced by sage-grouse habitat management actions, we calculated the size of each group I and group II reptile species' distribution and identified those with small distributions and a high proportion of distribution overlap with the range of the sage-grouse. We assumed that species with smaller distributions would be more sensitive to management actions because of the potential to affect (either positively or negatively) a greater proportion of the species' distribution and species with small distributions would tend to be more vulnerable to extinction (Pimm et al. 2014). We conducted a similar analysis to assess which species might be disproportionately affected by restoration or management actions because they have small distributions and a high proportion of their distribution within the sage-grouse range. We performed Bray-Curtis dissimilarity analyses in R using the vegan package (R Core Team 2017, Oksanen et al. 2018).

We created an additional metric to help distinguish the potential sensitivity of reptile species to sage-grouse habitat management by assuming that locations with greater levels of management actions targeting sage-grouse habitat may have increased effects on reptiles. Consequently, we calculated the proportion of the sage-grouse's range that is occupied by each reptile species (i.e., overlapping area of a given species divided by the range of the sage-grouse), and the proportion of each reptiles species' distribution falling within areas more likely to be protected or heavily managed for sage-grouse (Fig. 2). To represent these areas, we used priority habitat management areas (PHMAs; BLM 2017), which are areas designated in approved Resource Management Plans for each state (Landscape Data Approach Portal: https://landscape.blm.gov/geoportal/catalog, accessed 14 Jun 2019) and defined as the most valuable habitat for the greater sage-grouse. A relatively large overlap with these areas indicates the possibility of management decisions affecting the overlapping reptile species.

To better understand what habitat management actions are implemented in the range of the greater sage-grouse, we queried the Land Treatment Digital Library (LTDL; Pilliod and Welty 2013). The LTDL is a legacy dataset that houses historical BLM land treatments (Pilliod et al. 2017). The LTDL was recently updated to include all available land treatments occurring prior to 2015 within the range of the sage-grouse to provide information to the USFWS for the sage-grouse ESA listing decision in 2015. We ran 2 LTDL queries to extract the number of treatments that occurred between 1990 and 2014 in the range of sage-grouse, and within the PHMAs. Then we identified the number of treatments that were implemented to benefit sage-grouse by querying the database treatment-justification fields for the words sage and grouse. We also generated a summary report from the Conservation Efforts Database (USFWS 2014; conservationefforts.org, accessed 1 Oct 2018) to identify treatments specifically planned to benefit the greater sage-grouse on private and public lands (Heller et al. 2017). To provide the most reliable information, we chose to report information from these databases only for land treatments with implementation status that was confirmed in the field (Pilliod et al. 2017). Thus, combining information from both sources provides a sample (i.e., not a census) of all management actions, which represent minimum values for land area treated. Nonetheless, these land treatment summaries provide the types of treatments, relative amounts, and minimum areas treated in the range of the greater sage-grouse from 1990 to 2014.

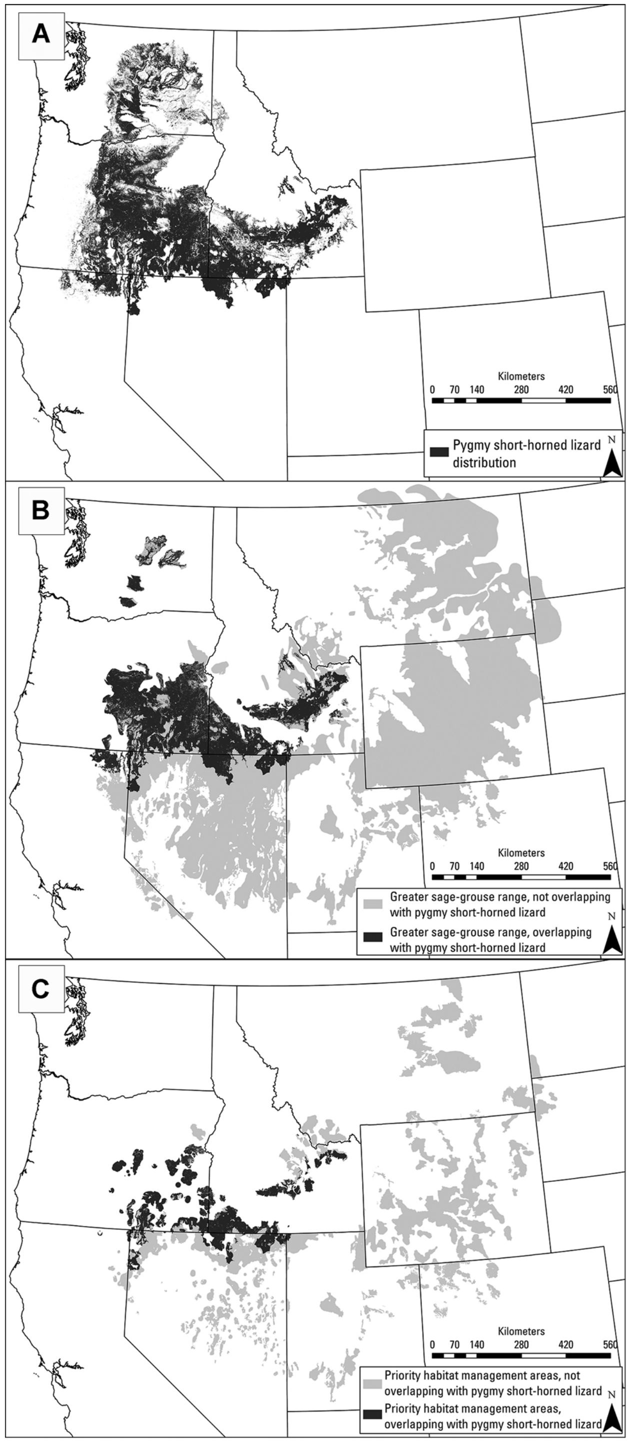

Figure 2. A) Distribution of an example reptile species (black); B) range of the greater sage-grouse in 2014 (gray), and the area of overlap with the example reptile species (black); and C) overlap (black) between the distribution of an example reptile species and the priority habitat management areas for greater-sage grouse (light gray). The example reptile used in these figures is the pygmy short-horned lizard in the western United States using modeled data, 2008–2013.

Finally, we conducted a literature search to assess how different reptile species might be affected by these various treatments. To search the literature, we used the words or terms sagebrush and reptile or snake or lizard or turtle, plus treatment, restoration, habitat management, seeding, grazing, conifer removal, mastication, or prescribed fire in Google Scholar (Google, Mountain View, CA, USA) on 3 June 2019. We reviewed the abstracts and text of each selection for inclusion of reptiles and relevance to the types of treatments that are conducted for sage-grouse. We then presented informative findings from past studies in a table for group I reptile species along with their observed relationships to several types of restoration or management actions (i.e., seeding, grazing, conifer removal). We also generated a table of the national and state-level conservation status of each group I reptile species to provide context for those species that are common and secure compared to those that are declining or at risk of extinction.

RESULTS

We mapped 190 reptile species in western North America. Species richness was generally highest in the southwest portion of the study area and lowest in the northeast (Fig. 1). Although the northeastern areas had lower species richness, richness was still surprisingly high, with some PHMAs in the northeast having as many as 13 reptile species (Fig. 1), mainly snakes. In contrast, the southwestern portion of the sage-grouse range had up to 35 species (Fig. 1), comprised equally of snakes and lizards (Order Squamata; Fig. S1, available online in Supporting Information). Nearly all of the sage-grouse range had ≥5 reptile species ($\bar{x} \pm$ SD richness across all pixels = 12.8 ± 5.6) and no areas were expected to be devoid of reptiles. The PHMAs had the same range of richness values (2–38 species) and a similar mean richness (12.2 ± 5.3 species) as the sage-grouse range.

Reptile Species That Might Benefit Under the Sage-Grouse Conservation Umbrella

Of the 190 reptile species, 70 (37%) overlapped with the range of the greater sage-grouse and 22 of those species overlapped substantially (i.e., they had >10% of their distribution within the sage-grouse range; Table 1). These included 11 snakes and 11 lizards but no turtles. Fourteen of these 22 (64%) substantially overlapping species shared similar land covers with sage-grouse (i.e., group I; Fig. 3). The remaining 8 substantially overlapping species occupied land covers that were less similar to sage-grouse habitat (i.e., group II; Fig. 3).

Using multiple criteria, such as species distribution size, distributional overlap with sage-grouse, and land cover similarity to sage-grouse, we ranked the species likely to benefit from sage-grouse conservation (Table 1; details provided in Table S2, available online in Supporting Information). Of the 14 group I species, the pygmy short-horned lizard (*Phrynosoma douglasii*) stood out from the rest with the largest percent of its distribution within the range of the greater sage-grouse (62.5%; Fig. 2B) and the highest similarity of land cover to sage-grouse (Table 1; Fig. 3). The remaining 13 group I species also may benefit from the sage-grouse conservation umbrella, but different factors influenced their rank and some tended to cluster together. The desert horned lizard (*Phrynosoma platyrhinos*), long-nosed leopard lizard (*Gambelia wislizenii*), tiger whiptail (*Aspidoscelis tigris*), western skink (*Plestiodon skiltonianus*), plains gartersnake (*Thamnophis radix*), and Arizona mountain kingsnake (*Lampropeltis pyromelana*) are good examples (Fig. 3). Some group II species have more distributional

Table 1. The 22 reptile species that overlap with the 2014 range of the greater sage-grouse by >10% of their distribution in the western United States using modeled distribution data, 2008–2016. We determined species ranks by the value of the composite distribution overlap and habitat similarity score (dividing the distribution overlap by the dissimilarity score). We calculated the proportion of distribution overlap as overlapping area between the reptile and sage-grouse divided by area of reptile distribution. We calculated land cover dissimilarity using the Bray-Curtis distance, where a value closer to zero indicates similarity, and a value closer to 1 indicates dissimilarity. An asterisk indicates the 14 species that are most likely to benefit under the conservation umbrella for sage-grouse on the basis of both proportion of their distribution overlapping with sage-grouse and land cover similarity with sage-grouse.

Common name	Proportional overlap of reptile distribution within the range of greater sage-grouse	Land cover dissimilarity score	Rank
Pygmy short-horned lizard*	0.625	0.199	1
Common sagebrush lizard*	0.380	0.296	2
Greater short-horned lizard*	0.326	0.334	3
Northern rubber boa*	0.344	0.396	4
Striped whipsnake*	0.273	0.341	5
Western fence lizard*	0.315	0.407	6
Desert nightsnake*	0.314	0.421	7
Western rattlesnake*	0.269	0.406	8
Desert horned lizard	0.324	0.522	9
Terrestrial gartersnake*	0.266	0.432	10
Common side-blotched lizard*	0.198	0.453	11
Gophersnake*	0.153	0.357	12
Great Basin collared lizard	0.232	0.564	13
Long-nosed leopard lizard	0.214	0.529	14
Prairie rattlesnake*	0.168	0.430	15
Plains hog-nosed snake	0.193	0.524	16
North American racer*	0.100	0.320	17
Western skink	0.147	0.563	18
Plateau fence lizard*	0.107	0.427	19
Tiger whiptail	0.146	0.586	20
Plains gartersnake	0.101	0.600	21
Arizona mountain kingsnake	0.105	0.706	22

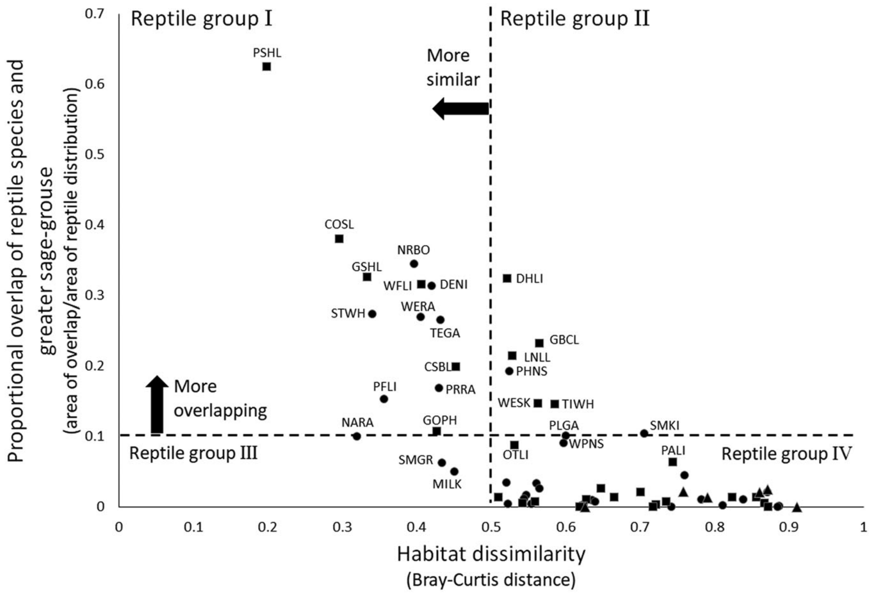

Figure 3. Reptile species that overlap with greater sage-grouse in the western United States and their land cover dissimilarity. We calculated the proportional overlap (*y*-axis) as the area of overlap (between each reptile distribution, 2008–2016, and the 2014 range of sage-grouse) divided by the distribution area of the reptile. The land cover dissimilarity (*x*-axis) values are Bray-Curtis distances between land cover proportions of each reptile and sage-grouse. A distance value closer to zero indicates greater similarity, whereas a value close to 1 indicates dissimilar land cover preferences. The vertical dashed line indicates the similarity threshold and the horizontal dashed line indicates the overlap threshold. Circles represent snakes, squares for lizards, and triangles for turtles. Species abbreviations are COSL = common sagebrush lizard, CSBL = common side-blotched lizard, DENI = desert nightsnake, DHLI = desert horned lizard, GBCL = Great Basin collared lizard, GOPH = gophersnake, GSHL = greater short-horned lizard, LNLL = long-nosed leopard lizard, MILK = milksnake, NARA = North American racer, NRBO = northern rubber boa, OTLI = ornate tree lizard, PALI = panamint alligator lizard, PFLI = plateau fence lizard, PHNS = plains hog-nosed snake, PLGA = plains gartersnake, PRRA = prairie rattlesnake, PSHL = pygmy short-horned lizard, SMGR = smooth green snake, SMKI = Arizona mountain kingsnake, STWH = striped whipsnake, TEGA = terrestrial gartersnake, TIWH = tiger whiptail, WERA = western rattlesnake, WESK = western skink, WFLI = western fence lizard, and WPNS = western patch-nosed snake.

overlap with sage-grouse than group I species and some of these had land cover similarity values close to our 0.5 Bray-Curtis threshold; these species, in particular, may also benefit from sage-grouse conservation. The milksnake (*Lampropeltis triangulum*) and smooth green snake (*Opheodrys vernalis*) fell just below the 10% threshold of distribution overlap but they share similar land cover as sage-grouse and thus could benefit in the few locations where they do overlap with sage-grouse (i.e., group III species; Fig. 3). Group IV species would be least likely to benefit by the sage-grouse conservation umbrella because they have the least overlap of ranges and least land cover similarity.

Reptile Species That Are Likely to Overlap with Management Actions Targeting Sage-Grouse

After evaluating the extent to which reptile species share space and land cover with sage-grouse, we next evaluated which species are more likely to be affected by restoration actions across the range of the sage-grouse (Fig. 4A). The North American racer (*Coluber constrictor*) and gophersnake (*Pituophis catenifer*) had large distributions and most (>65%) of the range of the sage-grouse was predicted to be occupied by these species (Fig. 4A). Hence, any management actions within the range of the sage-grouse might affect these 2 colubrid snakes, but their distributions are so large that the species are not particularly vulnerable range-wide, although local effects may still occur. In contrast, the pygmy short-horned lizard and plateau fence lizard (*Sceloporus tristichus*) were group I species with relatively small distributions, but only a small proportion of the range of the sage-grouse was predicted to be occupied by these species (Fig. 4A). Hence, across the range of the sage-grouse, management actions are less likely to affect these species because they occur only in a small portion of the sage-grouse range. Following this logic, the remainder (and majority) of group I species could be vulnerable to management actions because of the limited size of their distribution and how much of the sage-grouse's range is likely to be occupied by them (Fig. 4A). Notable species in this potentially affected group include common sagebrush lizard, greater short-horned lizard (*Phrynosoma hernandesi*), terrestrial gartersnake (*Thamnophis elegans*), and northern rubber boa (*Charina bottae*).

The common sagebrush lizard stood out within this group of species because it had a relatively small distribution and around 75% of the range of the sage-grouse was predicted to be occupied by this species. In other words, many habitat management decisions for sage-grouse have the potential to affect this species. On the other hand, much (62%) of the common sagebrush lizard distribution lies outside of the sage-grouse range and thus falls outside of management areas (Fig. 4B).

Group II species tend to have relatively small proportional overlap with sage-grouse and small distribution sizes (Fig. 4A). They are partly constrained to have less overlap

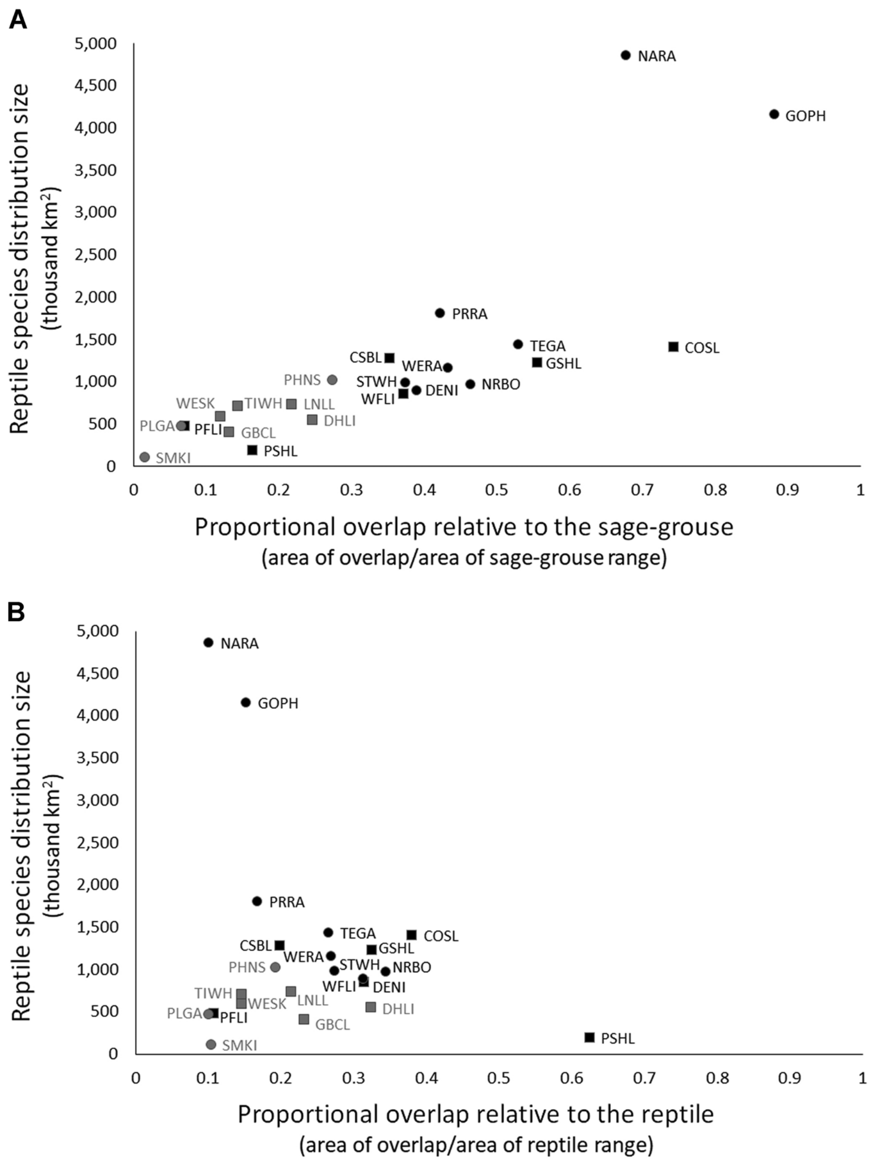

Figure 4. The relationship between distribution size of each reptile and overlap with the 2014 range of sage-grouse for the reptile species that share >10% distribution overlap with sage-grouse in the western United States. Reptile distribution used modeled data, 2008–2016. Group I species are represented in black and group II in gray. Panel A shows the overlap relative to the sage-grouse. We calculated the *x*-axis by the overlap (between each reptile and the range of sage-grouse) area divided by the area of the range of sage-grouse. Panel B shows the overlap relative to the reptile. The *x*-axis is calculated by the overlap (between each reptile and the range of the sage-grouse) area divided by the total area of the reptile distribution. The *y*-axis for both panels shows the distribution size for each reptile ($\times$1,000 km^2). The species included in reptile group I are those that overlap with sage-grouse (>10% of the reptile distribution overlaps) and have similar land cover proportions to sage-grouse (Bray-Curtis distance <0.5). The species included in reptile group II are those that overlap with sage-grouse (>10% of the reptile distribution overlaps) and have dissimilar land cover proportions to sage-grouse (Bray-Curtis distance >0.5). Snakes are represented as circles and lizards as squares. Species abbreviations are COSL = common sagebrush lizard, CSBL = common side-blotched lizard, DENI = desert nightsnake, DHLI = desert horned lizard, GBCL = Great Basin collared lizard, GOPH = gophersnake, GSHL = greater short-horned lizard, LNLL = long-nosed leopard lizard, NARA = North American racer, NRBO = northern rubber boa, PFLI = plateau fence lizard, PHNS = plains hog-nosed snake, PLGA = plains gartersnake, PRRA = prairie rattlesnake, PSHL = pygmy short-horned lizard, SMKI = Arizona mountain kingsnake, STWH = striped whipsnake, TEGA = terrestrial gartersnake, TIWH = tiger whiptail, WERA = western rattlesnake, WESK = western skink, WFLI = western fence lizard.

with sage-grouse by virtue of their use of relatively dissimilar land covers to those used by the bird.

Reptile Species That Could Be Disproportionately Affected by Management Actions Targeting Sage-Grouse

When we plotted reptile distribution size versus proportional distribution overlap, this time relative to the distribution of each reptile (Fig. 4B) as opposed to relative to the sage-grouse range, the pygmy short-horned lizard stood out because it has the smallest distribution of any group I reptile examined and 62.5% of its range is contained within the sage-grouse range. Therefore, where the lizard occurs, management actions targeting sage-grouse habitat could have a disproportionately large effect on this lizard because it has such a small distribution and the majority of it lies within the range of the sage-grouse. Eight other group I species clustered together (Fig. 4B) with relatively small distribution sizes and 25–40% of their distribution area overlapping with the sage-grouse range: common sagebrush lizard, greater short-horned lizard, western fence lizard (*Sceloporus occidentalis*), northern rubber boa, striped whipsnake (*Coluber taeniatus*), desert nightsnake (*Hypsiglena chlorophaea*), western rattlesnake (*Crotalus oreganus*), and terrestrial gartersnake. Common side-blotched lizard (*Uta stansburiana*) and prairie rattlesnake (*Crotalus viridis*) tended to align more closely with some group II species (Fig. 4B), including long-nosed leopard lizard, Great Basin collared lizard (*Crotaphytus bicinctores*), and plains hog-nosed snake (*Heterodon nasicus*).

Because habitat management is unlikely to be uniformly distributed across the range of the sage-grouse, we then focused on potential effects (both positive and negative) to reptiles within PHMAs; areas most likely to be managed specifically for sage-grouse habitat and population persistence. When we assessed reptiles within PHMAs, species clustered similarly to how they clustered across the entire range of the sage-grouse. This indicates that reptile species' area of overlap with PHMAs and the entire sage-grouse range are correlated, and that species' relationships with PHMAs are representative of those across the sage-grouse's range (Fig. S2, available online in Supporting Information).

Prevalence of Management Actions Targeting Sage-Grouse

From 1990 to 2014, ≥6,400 land treatments covering about 4 million ha have occurred on BLM land within the range of the greater sage-grouse (Table 2). Approximately a third of these treatments were implemented with sage-grouse cited as a specific justification for the management action. Nearly 40% of these land treatments occurred within PHMAs, despite PHMAs only comprising about a third of the sage-grouse range. Within PHMAs, 44% of treatments implemented from 1990 to 2014 were undertaken to benefit sage-grouse specifically. Overall, vegetation seeding accounted for 41% of the treatments and 65% of the area treated (Table 2). Most of these seedings were post-fire treatments. Improving sage-grouse habitat is usually a secondary goal of these post-fire seedings with the main goal to prevent burned areas from further degrading (e.g., being dominated by non-native, annual grasses and forbs).

In addition to LTDL data, 6,022 records in the Conservation Efforts Database (CED) described sage-grouse habitat conservation actions occurring on approximately 1.25 million ha of private and public lands from 2000 to 2014 (some of these treatments overlap with those in the LTDL database). Consistent with treatments on BLM lands, about 40% of the conservation efforts reported in the CED occurred within the PHMAs. The 2 most frequent conservation efforts documented in the CED were vegetation management and habitat enhancement (2,639 actions, 43.8% of all records) and conifer removal (1,032 actions, 17% of all records). In contrast to the post-fire seeding treatments described above, the primary goal of these types of treatments often is to improve existing sage-grouse habitat explicitly. It is important to consider that these values are minimums because we were confident reporting only treatments verified as fully implemented or completed in the LTDL and CED from 1990 to 2014 or from 2000 to 2014, respectively. Also, these databases are not a census of all treatments implemented and additional management actions have occurred since. For example, in Utah, 233,500 ha of public and private land have been treated or are planned to be treated in sage-grouse management areas between 2008 and 2020 (www.wri.utah.gov, accessed 18 Sep 2019). Many of these treatments focused or will focus on removal of pinyon and juniper woodlands (20%) and sagebrush restoration (27%).

Potential Response of Reptiles to Sage-Grouse Management Actions

We did not locate any studies documenting the effects of sage-grouse-specific habitat restoration or management on reptiles. We found 9 studies that examined our group I or II species regarding response to land treatments that were somewhat similar to those implemented for sage-grouse: seeding to control invasives (crested wheatgrass [*Agropyron cristatum*] seeding), targeted grazing to reduce risk of wildfire (grazing), and pinyon-juniper removal to reduce

Table 2. Land treatments conducted in the western United States, 1990–2014, on lands administered by the Bureau of Land Management within and immediately adjacent to the 2014 range of the greater sage-grouse in the United States. Treatment counts are reported from treatments in the Land Treatment Digital Library (Pilliod and Welty 2013) that have a polygon, point, or line feature, but area treated (ha) is reported only from treatments with polygon features. We calculated the percent of treated area by dividing the area for a treatment category by the area treated. We included only land treatments with confirmed implementation; thus, these counts and areas represent minimums.

	Confirmed implemented treatments			Treatments for sage-grouse		
Treatment category	Treatment count	Area treated (ha)	% of treated area	Treatment count	Area treated (ha)	% of treated area
Seedings	2,657	2,556,361	65	1,072	1,144,777	70
Prescribed burns	910	400,472	10	177	106,834	6
Vegetation disturbance[a]	914	238,553	6	233	82,491	5
Herbicide	691	356,168	9	161	121,399	7
Other	554	159,434	4	201	111,665	7
Soil disturbances[b]	427	160,848	4	135	38,835	2
Juniper or pinyon-juniper removal	317	72,913	2	116	37,802	2
Total	6,470	3,944,749	100	2,095	1,643,804	100

[a] Mastication, thinning, other than juniper and pinyon-juniper removal.
[b] Plowing, chaining.

Table 3. Reptile associations with land treatments typically implemented for greater sage-grouse in sagebrush ecosystems of the western United States using literature, 1970–2019. We included species if they overlap with greater sage-grouse by >10% of their modeled distributions (i.e., group I and II species, 2008–2016) and have some literature available on associations with treatments. For each treatment, we indicate a positive association (P), a negative association (N), no association observed (0), or no information available from the literature (.).

Common name	Crested wheatgrass seeding	Grazing[a]	Conifer felling	Citations
Pygmy short-horned lizard	N	P	.	Reynolds (1979), Reynolds and Trost (1980), Werschkul (1982)
Common sagebrush lizard	N	N	P	Reynolds (1979), Reynolds and Trost (1980), Werschkul (1982), James and M'Closkey (2003), Beever and Brussard (2004)
Greater short-horned lizard	N	.	.	Hanser et al. (2011)
Western fence lizard	N	0	.	Werschkul (1982), James and M'Closkey (2003), Beever and Brussard (2004)
Western rattlesnake	N	.	.	Jochimsen et al. (2014)
Desert horned lizard	N	P, N	.	Werschkul (1982), Beever and Brussard (2004), Newbold and MacMahon (2008)
Common side-blotched lizard	N	N	P	Werschkul (1982), James and M'Closkey (2003), Beever and Brussard (2004)
Gophersnake	N	.	.	Jochimsen et al. (2014)
Great Basin collared lizard	N	P	.	Werschkul (1982), Beever and Brussard (2004)
Long-nosed leopard lizard	N	.	.	Werschkul (1982)
Tiger whiptail	N	P, N	.	Werschkul (1982), Beever and Brussard (2004), Germano et al. (2012)

[a] Grazing treatments are experimental and vary by study. Review of the treatment specifications is important for interpretation of grazing effects and effects of other treatments.

wildfire risk or limit predator perching and nesting habitat (conifer felling; Table 3). About half of these studies compared treated to untreated areas or made before-after comparisons, whereas the remaining studies only documented habitat associations. Careful interpretation of these findings is warranted relative to the experimental design, the level inference, the specifics about each treatment, the landscape context, and how these studies assessed species-habitat relationships.

With such limited information and uncertainty about reptile responses, future restoration projects may also want to prioritize monitoring of species that could occur in a project area on the basis of their conservation status (Table 4). Of the 70 reptile species with ranges overlapping the greater sage-grouse, 66 are currently considered stable across their geographic range (IUCN least concern; Table S3, available online in Supporting Information). The remaining 4 include 2 lizards, a turtle, and a tortoise. The Gila monster (*Heloderma suspectum*) is listed as near threatened—decreasing and the panamint alligator lizard (*Elgaria panamintina*) is listed as vulnerable—decreasing, but neither of these species have distributions that overlap with the range of sage-grouse by >10% and their habitat associations do not overlap with those of the bird (i.e., group IV species; Fig. 3, Tables S2, S3). The northwestern pond turtle (*Actinemys marmorata*) and Mojave desert tortoise (*Gopherus agassizii*) are listed as vulnerable, but they also did not meet our criteria for inclusion under the sage-grouse umbrella (Tables S2, S3). The Mojave desert tortoise is the only species of our 70 that is listed as a threatened species under the ESA. Therefore, most of the reptiles in the range of the sage-grouse are off the radar for conservation priorities in sagebrush ecosystems because they are considered stable globally and have no federal mandates for protection in the United States. Several species, however, have state conservation status (Table 4).

DISCUSSION

Our findings confirm that the greater sage-grouse qualifies as a potential umbrella species for sagebrush ecosystems, meeting the basic requirement for having a large distribution relative to those of potential beneficiary species under the umbrella (Wilcox 1984). The greater sage-grouse range in western North America is shared with a wide variety of vertebrates, with estimates ranging from 250 to 350 species (Sands et al. 1999), including 70 reptile species that we identified in our assessment. This suggests that 20–28% of vertebrates that co-occur with sage-grouse, and potentially fall under the sage-grouse conservation umbrella, are reptiles, specifically snakes and lizards.

Other sage-grouse umbrella assessments have included reptiles but only for a subset of species that were considered sagebrush obligates or associates (Rowland et al. 2006, Carlisle et al. 2018*b*, Runge et al. 2019), and often with results that were inconsistent with each other and our findings. We examine some of these similarities and differences more closely.

Table 4. The conservation status of the 22 reptile species that overlap with the 2014 range of the greater sage-grouse by >10% of their distribution in the western United States, 2008–2016. Global and national rankings include International Union for the Conservation of Nature (IUCN), Committee on the Status of Endangered Wildlife in Canada (COSEWIC), and the Endangered Species Act (ESA) of the United States. Asterisks indicate the 14 species that are most likely to benefit under the conservation umbrella for greater sage-grouse on the basis of both proportion of their distribution overlapping with sage-grouse and habitat similarity with sage-grouse (group I species). For the United States, we list only the western states where sage-grouse occur and have species status of S1–S3, or I–II. State rankings include critically imperiled (S1), imperiled (S2), rare or uncommon (S3), not rare and apparently secure (S4), and demonstrably widespread (S5) in Idaho, Montana, Nevada, Utah, and Washington. Species designations in North Dakota and South Dakota are described as levels with the following definitions: I = high level of conservation priority, II = moderate level of conservation priority or a high conservation priority but with substantial funding available for the species, III = moderate level of conservation priority but are believed to be peripheral or non-breeding in North Dakota. Oregon species are listed as sensitive or sensitive-critical. Wyoming species have the addition of a state level endangerment designation, such as those listed under the ESA. Wyoming species designations tiers are I = highest priority, II = moderate priority, and III = lowest priority. A dash indicates no available information.

Common name	IUCN and NatureServe	COSEWIC	ESA	State status*
Pygmy short-horned lizard*	Least concern	Extirpated	Not listed	II (ND), S3 (WA)
Common sagebrush lizard*	Least concern	—	Not listed	S2 (SD), S3 (WA)
Greater short-horned lizard*	Least concern	Special concern	Not listed	S2 (SD), II (WY), S3 (ID), S3S4 (NV)
Northern rubber boa*	Least concern	Special concern	Not listed	II (WY), S3S4 (NV)
Striped whipsnake*	Least concern	—	Not listed	S1 (WA)
Western fence lizard*	Least concern	—	Not listed	—
Desert nightsnake*	Least concern	Endangered	Not listed	—
Western rattlesnake*	Least concern	Threatened	Not listed	Sensitive-critical (OR)
Desert horned lizard	Least concern	—	Not listed	—
Terrestrial gartersnake*	Least concern	—	Not listed	—
Common side-blotched lizard*	Least concern	—	Not listed	S3 (WA)
Gophersnake*	Least concern	—	Not listed	—
Great Basin collared lizard	Least concern	—	Not listed	S2 (ID)
Long-nosed leopard lizard	Least concern	—	Not listed	—
Prairie rattlesnake*	Least concern	Special concern	Not listed	—
Plains hog-nosed snake	Least concern	—	Not listed	I (ND), II (WY), S2 (MT)
North American racer*	Least concern	—	Not listed	—
Western skink	Least concern	Special concern	Not listed	—
Plateau fence lizard*	—	—	Not listed	—
Tiger whiptail	Least concern	—	Not listed	—
Plains gartersnake	Least concern	—	Not listed	—
Arizona mountain kingsnake	Least concern	—	Not listed	S2 (NV), S3 (UT)

Reptile Species That Might Benefit Under the Sage-Grouse Conservation Umbrella

Our findings suggest that 37% of reptile species in the western United States and Canada have ranges that fall within at least some portion of the range of the greater sage-grouse, implying that about a third of all reptiles in the region could benefit, at least to some extent, if sage-grouse habitat is protected or improved. We suspect the percentage of potential beneficiary reptile species may be closer to 7–12% (14–22 species) given the habitat requirements and distribution overlap thresholds (>10%) that we identified from the pool of 190 reptile species within the range of the bird.

A previous assessment concluded that management of sage-grouse habitat in the Great Basin likely would offer little conservation benefit for reptiles because of dissimilar land cover affinities and small range overlaps between reptiles and sage-grouse compared to other vertebrates (Rowland et al. 2006). Using independent data sources, both Rowland et al. (2006) and our study reported that the common sagebrush lizard, considered a sagebrush obligate by some (Rowland et al. 2006), was likely to benefit from sage-grouse conservation on the basis of range overlap and habitat preferences. Our assessment, however, was that the pygmy short-horned lizard was the most likely to benefit under the sage-grouse umbrella, based on range overlap and habitat similarity with sage-grouse. Nevertheless, both the pygmy short-horned lizard and common sagebrush lizard are associated with sagebrush communities, especially where understory is sandy and free from dense grasses that impede their foraging movements (Reynolds 1979, Green et al. 2001, James and M'Closkey 2002).

One difference between other sage-grouse umbrella species assessments and ours is that no other study has examined all reptile taxa across the entire range of the greater sage-grouse. This difference can influence study conclusions because of local (e.g., state) versus regional (multi-state or range-wide) differences in species compositions and associations with sage-grouse habitat. For example, in Wyoming, researchers concluded that, among all reptiles in the state, only the greater short-horned lizard would benefit from the protection of sage-grouse conservation areas (Carlisle et al. 2018*b*). Greater short-horned lizards are associated with big sagebrush in Wyoming (Hanser et al. 2011) and we also identified it among the group I beneficiary species as third most likely to benefit across the entire range of the greater sage-grouse based on area and land cover overlap characteristics. Comparisons of state-specific to range-wide assessments may be informative to understand relative importance of portions of species' ranges, and how these may contribute to the whole. Afterall, reptiles in the United States are managed in the public trust by state governments and thus state-level assessments are meaningful, especially for species not listed under the ESA (Tables 4 and S3).

Although we distinguished group I and II species for purposes of ranking, we suspect that group II species might also benefit from sage-grouse conservation on more of a regional scale or as spillover from adjacent habitat restoration activities even though their land cover associations are relatively different from those of the sage-grouse. Similar to our findings, Rowland et al. (2006) identified some of our group II species as having habitat preferences that were not particularly similar to those of the sage-grouse, or in the case of the Great Basin collared lizard, habitat preferences were distinct from those of sage-grouse. Many of these group II species are active foragers that need open interspaces between shrubs and the structure provided by shrubs, shrub islands, and rock outcroppings (Werschkul 1982). The reliance of species on microhabitats complicates broad-scale range overlap and umbrella species assessments (Rowland et al. 2006) and can be a shortcoming of overlap studies such as ours.

Reptile Species That Are Likely to Overlap with or Could Be Disproportionately Affected by Management Actions Targeting Sage-Grouse

Management actions targeting sage-grouse habitat where pygmy short-horned lizards occur could have a disproportionately large effect on this lizard because it has a small distribution, the majority of which lies within the sage-grouse range. Eight other group I species also warrant attention because they have relatively small distribution sizes and 25–40% of their distribution area overlap with the sage-grouse range. Most notable in this group are the common sagebrush lizard, northern rubber boa, and greater short-horned lizard, which ranked highly from both the sage-grouse perspective (Fig. 4A) and the reptile perspective (Fig. 4B). Range size is one of the most important predictors of extinction risk among reptiles (Böhm et al. 2016). Thus, a manager may want to be particularly aware of the habitat requirements for species with limited distributions at the state or regional level when considering habitat management actions where they are likely to occur.

Central to prioritizing species under the sage-grouse umbrella is also understanding their distribution beyond the range of the sage-grouse. A good example of this is the gophersnake, which has a distribution overlapping 88% of the range of the greater sage-grouse, but this portion comprises only 15% of the snake's distribution. This pattern was also evident in a study in Wyoming where the gophersnake overlapped with 29% of the reserves created for sage-grouse, but these greater sage-grouse conservation areas did not provide a protected area for gophersnakes that was better than one selected at random (Carlisle et al. 2018*b*). Species such as the gophersnake could easily fall in the trap of dismissal by resource managers because of their patterns of distributional overlap with sage-grouse. In other words, an overlap of 15% range-wide or nearly 30% within protected areas of a state may not be considered particularly meaningful for the conservation of a widely distributed reptile species. From a smaller scale perspective (e.g., such as a county or even a state), however, the habitat management actions conducted in the area where the species occurs could still have major implications for the reptile species (Pike et al. 2011). This exemplifies how studies of species overlap can be insightful and misleading and how the task of ranking potential beneficiary species under single-species umbrella management is multi-faceted, complex, and requires careful consideration of scale and local or regional context.

Management Actions Targeting Sage-Grouse and Potential Reptile Responses

Land treatments conducted from 1990 to 2014 were primarily seedings. In the Great Basin, previous assessments have found that sagebrush was the most frequently seeded shrub and crested wheatgrass was the most frequently seeded grass (Pilliod et al. 2017). About a quarter of the seeding treatments in the range of the sage-grouse have included crested wheatgrass, which could be problematic for snakes and lizards who appear to avoid these non-native grasslands (Reynold and Trost 1980; Table 3) or for those that require shrub canopies, the development of which may be hindered by dense stands of highly competitive grasses such as crested wheatgrass (Gunnell et al. 2010, Knutson et al. 2014). Some of these seedings, however, are intended to reduce non-native annual grasses, such as cheatgrass, which for similar reasons, could be potentially more problematic than crested wheatgrass, particularly for lizards (Green et al. 2001, Newbold 2005, Rieder et al. 2010, Runge et al. 2019). The goal of restoring native shrubland vegetation following human or natural disturbances across the range of the sage-grouse provides an exciting opportunity to better assess how reptile species and communities (e.g., lizard-eating snakes such as the striped whipsnake or desert nightsnake) respond to such intervention.

The next step in predicting how species might benefit under the sage-grouse umbrella is to improve understanding of how species might be affected by habitat modifications that are likely to occur under single-species management. Ideally, empirical evidence would be available from controlled, experimental studies of management actions aimed at restoring sage-grouse habitat for each of the 14 to 22 beneficiary reptile species that we identified (i.e., group I and II species). A review of the literature, however, revealed that few studies exist, despite the considerable legacy of land treatments conducted for sage-grouse on public and private lands. This lack of information on population responses to habitat management and loss is typical for reptiles in the United States and around the world and it presents a major conservation challenge (Böhm et al. 2013).

Although the available information on reptile responses to sage-grouse habitat management is weak to non-existent presently, many of the land cover associations between reptiles and sage-grouse that we identified were somewhat similar. In other words, the correlative patterns (Table 3) for reptiles are fairly representative of greater sage-grouse habitat preferences, including preferring intact stands of sagebrush with relatively low amounts of introduced grasses (e.g., crested wheatgrass, cheatgrass) or conifers (Arkle et al. 2014, Farzan et al. 2015). Conifer felling and removal (i.e., of pinyon pine and juniper trees encroaching into sagebrush) is one of the most common habitat management actions used to reduce perching and nesting structures for avian predators of sage-grouse and reduce wildfire risk (Farzan et al. 2015, Bombaci and Pejchar 2016, Holmes et al. 2017). James and M'Closkey (2003) reported a positive response from 2 lizard species within our group I list (common sagebrush lizard and common side-blotched lizard) when the trees were cut and left on site because these species preferred dead over live trees regardless of whether they were standing or prone. Given their tendency to use pinyon and juniper trees for perching, removal (instead of just felling) of this habitat structure could have a negative effect on some of these lizards (Morrison and Hall 1999). Removal of conifers to improve sage-grouse habitat, however, could also benefit many other lizard and snake species that prefer open sagebrush shrublands and are also susceptible to avian predators. Finally, similar to sage-grouse, reptiles appear to have mixed responses to grazing because of variation in timing, frequency, and duration of grazing, and livestock type, stocking rate, and other factors (Beck and Mitchell 2000, Dettenmaier et al. 2017).

We found no published studies examining the effects of prescribed fire on our group I or II reptile species, although this treatment type is generally uncommon within the range of the sage-grouse. Research in low-elevation sagebrush steppe suggests that post-wildfire landscapes may support fewer tiger whiptails and striped whipsnakes, and more North American racers (Cossel 2003). It is difficult to compare effects of prescribed fire and wildfire and these reptiles may also be responding to the loss of shrublands and conversion to annual grasslands more than the direct effects of fire. In fact, none of the studies we examined assessed effects of restoration actions relative to a no-action alternative in an experimental design. This is important because our data show that most land treatments are implemented in response to wildfire (e.g., post-fire seeding) to mitigate against an ecological-state transition into an undesirable habitat condition. In other words, it is possible that no-intervention for sage-grouse could also have ecological implications for reptiles, especially when rates of shrubland recovery are so slow (Lesica et al. 2007, Knutson et al. 2014, Avirmed et al. 2015).

Thus, because of insufficient information, we could not make defendable conclusions regarding the effects of specific management actions on reptiles, as a whole or for individual species. The effects of habitat management actions on reptiles will likely depend on the disturbance history of a site, its condition prior to intervention, and the species present or available to colonize or recolonize from adjacent areas. This variability complicates study-level generalities for specific treatment effects on individual species. Overall, however, the agreement among species in their response to habitat management as reported in the literature (Table 3) suggests that habitat management actions intended for sage-grouse may have similar responses by grouse and reptiles. If true, this would fulfill the third criteria of the umbrella species concept; restoration or management actions targeting the umbrella species should also benefit, or at least not negatively affect, co-occurring species.

Although the reptile species in the range of the greater sage-grouse are apparently stable globally, several species may warrant attention because of regional declines, other threats, rarity, or data deficiency. For example, of the 14 group I species that we identified as potential beneficiaries under the sage-grouse umbrella, 6 were ranked as either extirpated, endangered, threatened, or of special concern in Canada and 7 had conservation status within specific states (Table 4). Many of these conservation concerns appear to be associated with the periphery of species' ranges. Still, documented declines, rarity, and a lack of empirical information about the status of most species suggests that keeping our short-list of species on the watch list for several states is warranted. The lack of data on status and trends for most reptiles is particularly concerning.

MANAGEMEMT IMPLICATIONS

We anticipated providing a definitive list of reptile species that could be classified as sagebrush obligate or sagebrush associate and thus would be included in various conservation efforts across the sagebrush biome. We found, however, that this simplistic designation is not so useful. Instead, we identified 14 (group I) reptile species that warrant additional consideration when planning habitat restoration or making management decisions within sage-grouse habitat. We consider this list a reasonable starting point given the range, distribution, and habitat associations of lizards, snakes, turtles, and tortoises within the range of the greater sage-grouse. Of this list, we found that the pygmy short-horned lizard and common sagebrush lizard stood out from the others, warranting closer attention. Currently, however, there is insufficient evidence to assess the specific effects of sage-grouse habitat management actions on these or any of the lizard and snake species across the western United States. Although it is optimistic to expect that habitat management decisions intended for sage-grouse will benefit these and other species under the sage-grouse umbrella, further empirical evidence is needed to confirm this expectation.

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LITERATURE CITED

Andelman, S. J., and W. F. Fagan. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences of the United States of America 97:5954–5959.

Arkle, R. S., D. S. Pilliod, S. E. Hanser, M. L. Brooks, J. C. Chambers, J. B. Grace, K. C. Knutson, D. A. Pyke, J. L. Welty, and T. A. Wirth. 2014. Quantifying restoration effectiveness using multi-scale habitat models: implications for sage-grouse in the Great Basin. Ecosphere 5:1–32.

Avirmed, O., W. K. Lauenroth, I. C. Burke, and M. L. Mobley. 2015. Sagebrush steppe recovery on 30–90-year-old abandoned oil and gas wells. Ecosphere 6:1–10.

Beck, J. L., J. W. Connelly, and C. L. Wambolt. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. Rangeland Ecology and Management 65:444–455.

Beck, J. L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage grouse habitat. Wildlife Society Bulletin 28:993–1002.

Beever, E. A., and P. F. Brussard. 2004. Community-and landscape-level responses of reptiles and small mammals to feral-horse grazing in the Great Basin. Journal of Arid Environments 59:271–297.

Belton, L. R., and D. Jackson-Smith. 2010. Factors influencing success among collaborative sage-grouse management groups in the western United States. Environmental Conservation 37:250–260.

Böhm, M., B. Collen, J. E. Baillie, P. Bowles, J. Chanson, N. Cox, G. Hammerson, M. Hoffmann, S. R. Livingstone, M. Ram, and A. G. Rhodin. 2013. The conservation status of the world's reptiles. Biological Conservation 157:372–385.

Böhm, M., R. Williams, H. R. Bramhall, K. M. McMillan, A. D. Davidson, A. Garcia, L. M. Bland, J. Bielby, and B. Collen. 2016. Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Global Ecology and Biogeography 25:391–405.

Bombaci, S., and L. Pejchar. 2016. Consequences of pinyon and juniper woodland reduction for wildlife in North America. Forest Ecology and Management 365:34–50.

Branton, M., and J. S. Richardson. 2011. Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. Conservation Biology 25:9–20.

Bureau of Land Management [BLM]. 2017. BLM Western U.S. GRSG ARMP and ARMPA Habitat Management Areas, October 2017 Update. <https://gis.blm.gov/GRSGEISDownload/Layerpackages/BLM_ARMP_ARMPA_GRSG_HMA_Oct2017_Update.lpk>. Accessed 1 May 2018.

Carlisle, J. D., A. D. Chalfoun, K. T. Smith, and J. L. Beck. 2018*a*. Non-target effects on songbirds from habitat manipulation for greater sage-grouse: implications for the umbrella species concept. Condor 120:439–455.

Carlisle, J. D., D. A. Keinath, S. E. Albeke, and A. D. Chalfoun. 2018*b*. Identifying holes in the greater sage-grouse conservation umbrella. Journal of Wildlife Management 82:948–57.

Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. Conservation Biology 13:805–814.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–68 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, volume 38. University of California Press, Berkeley, USA.

Copeland, H. E., H. Sawyer, K. L. Monteith, D. E. Naugle, A. Pocewicz, N. Graf, and M. J. Kauffman. 2014. Conserving migratory mule deer through the umbrella of sage-grouse. Ecosphere 5(9):1–16.

Cossel, J. O., Jr. 2003. Changes in reptile populations in the Snake River Birds of Prey Area, Idaho between 1978–79 and 1997–98: the effects of weather, habitat, and wildfire. Dissertation, Idaho State University, Pocatello, USA.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2–19.

Crother, B. I. 2017. Scientific and standard English names of amphibians and reptiles of North America north of Mexico, with comments regarding confidence in our understanding. Eighth edition. Society for the Study of Amphibians and Reptiles Herpetological Circulars 43:1–104.

Cushman, S. A., K. S. McKelvey, B. R. Noon, and K. McGarigal. 2010. Use of abundance of one species as a surrogate for abundance of others. Conservation Biology 24:830–840.

Dettenmaier, S. J., T. A. Messmer, T. J. Hovick, and D. K. Dahlgren. 2017. Effects of livestock grazing on rangeland biodiversity: a meta-analysis of grouse populations. Ecology and evolution 7:7620–7627.

Donnelly, J. P., J. D. Tack, K. E. Doherty, D. E. Naugle, B. W. Allred, and V. J. Dreitz. 2017. Extending conifer removal and landscape protection strategies from sage-grouse to songbirds, a range-wide assessment. Rangeland Ecology and Management 70:95–105.

Duvall, A. L., A. L. Metcalf, and P. S. Coates. 2017. Conserving the greater sage-grouse: a social-ecological systems case study from the California-Nevada region. Rangeland Ecology and Management 70: 129–140.

Evans, D. M., J. P. Che-Castaldo, D. Crouse, F. W. Davis, R. Epanchin-Niell, C. H. Flather, R. K. Frohlich, D. D. Goble, Y.-W. Li, T. D. Male, et al. 2016. Species recovery in the United States: increasing the effectiveness of the Endangered Species Act. Issues in Ecology 20:1–27.

Farzan, S., D. J. Young, A. G. Dedrick, M. Hamilton, E. C. Porse, P. S. Coates, and G. Sampson. 2015. Western juniper management: assessing strategies for improving greater sage-grouse habitat and rangeland productivity. Environmental Management 56:675–683.

Germano, D. J., G. B. Rathbun, and L. R. Saslaw. 2012. Effects of grazing and invasive grasses on desert vertebrates in California. Journal of Wildlife Management 76:670–682.

Green, G. A., K. B. Livezey, and R. L. Morgan. 2001. Habitat selection by northern sagebrush lizards (*Sceloporus graciosus graciosus*) in the Columbia Basin, Oregon. Northwestern Naturalist 82:111–115.

Gunnell, K. L., T. A. Monaco, C. A. Call, and C. V. Ransom. 2010. Seedling interference and niche differentiation between crested wheatgrass and contrasting native Great Basin species. Rangeland Ecology and Management 63:443–449.

Hanser, S. E., and S. T. Knick. 2011. Greater sage-grouse as an umbrella species for shrubland passerine birds: a multiscale assessment. Pages 475–487 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. University of California Press, Berkeley, USA.

Hanser, S. E., M. Leu, C. L. Aldridge, S. E. Nielsen, M. M. Rowland, and S. T. Knick. 2011. Occurrence and abundance of ants, reptiles, and mammals. Pages 221–314 *in* M. Leu, S. T. Knick, and C. L. Aldridge, editors. Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, Kansas, USA.

Heller, M. M., J. Welty, and L. A. Wiechman. 2017. The Conservation Efforts Database: improving our knowledge of landscape conservation actions. Great Northern Landscape Conservation Cooperative, Bozeman, Montana, USA.

Holmes, A. L., J. D. Maestas, and D. E. Naugle. 2017. Bird responses to removal of western juniper in sagebrush-steppe. Rangeland Ecology and Management 70:87–94.

International Union for Conservation of Nature [IUCN]. 2017. The IUCN Red List of Threatened Species. Version 2017-3. <http://www.iucnredlist.org>. Accessed 23 May 2017.

James, S. E., and R. T. M'Closkey. 2002. Patterns of microhabitat use in a sympatric lizard assemblage. Canadian Journal of Zoology 80:2226–2234.

James, S. E., and R. T. M'Closkey. 2003. Lizard microhabitat and fire fuel management. Biological Conservation 114:293–297.

Jochimsen, D. M., C. R. Peterson, and L. J. Harmon. 2014. Influence of ecology and landscape on snake road mortality in a sagebrush-steppe ecosystem. Animal Conservation 17:583–592.

Johnson, S. A., H. K. Ober, and D. C. Adams. 2017. Are keystone species effective umbrellas for habitat conservation? A spatially explicit approach. Journal for Nature Conservation 37:47–55.

Knick, S. T., and J. W. Connelly. 2011. Greater sage-grouse and sagebrush—an introduction to the landscape. Pages 1–9 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, volume 38. University of California Press, Berkeley, USA.

Knutson, K. C., D. A. Pike, T. A. Wirth, R. S. Arkle, D. S. Pilliod, M. L. Brooks, J. C. Chambers, and J. B. Grace. 2014. Longer-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. Journal of Applied Ecology 51:1414–1424.

Krysko, K. L., L. P. Nuñez, C. E. Newman, and B. W. Bowen. 2017. Phylogenetics of kingsnakes, *Lampropeltis getula* Complex (Serpentes: Colubridae), in Eastern North America. Journal of Heredity 108: 226–238.

Leache, A. 2009. Species tree discordance traces to phylogeographic clade boundaries in North American fence lizards (*Sceloporus*). Systematic Biology 58:547–559.

Lesica, P., S. V. Cooper, and G. Kudray. 2007. Recovery of big sagebrush following fire in southwest Montana. Rangeland Ecology and Management 60:261–269.

Lindstrom, J. 2014. Greater sage-grouse 2015 USFWS status review current range. U.S. Geological Survey data release. <https://gis1.usgs.gov/arcgis/rest/services/sage_web_app/GRSG_2015_USFWS_StatusReview_CurrentRange/MapServer>. Accessed 1 May 2018.

McAdoo, J. K., S. R. Swanson, B. W. Schultz, and P. F. Brussard. 2004. Vegetation management for sagebrush-associated wildlife species. Pages 189–193 *in* A. L. Hild, N. L. Shaw, S. E. Meyer, D. T. Booth, and E. D. McArthur, editors. Seed and soil dynamics in shrubland ecosystems. Proceedings RMRS-P-31. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Morrison, M. L., and L. S. Hall. 1999. Habitat characteristics of reptiles in pinyon-juniper woodland. Great Basin Naturalist 59:288–291.

Murphy, T., D. E. Naugle, R. Eardley, J. D. Maestas, T. Griffiths, M. Pellant, and S. J. Stiver. 2013. Trial by fire: improving our ability to reduce wildfire impacts to sage-grouse and sagebrush ecosystems through accelerated partner collaboration. Rangelands 35(3):2–10.

Nafis, G. 2018. California herps—A guide to the amphibians and reptiles of California. <http://www.californiaherps.com/>. Accessed 1 May 2018.

Newbold, T. A. S. 2005. Desert horned lizard (*Phrynosoma platyrhinos*) locomotor performance: the influence of cheatgrass (*Bromus tectorum*). Southwestern Naturalist 50:17–23.

Newbold, T. S., and J. A. MacMahon. 2008. Consequences of cattle introduction in a shrubsteppe ecosystem: indirect effects on desert horned lizards (*Phrynosoma platyrhinos*). Western North American Naturalist 68:291–303.

Oksanen, J., F. Guillaume Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, et al. 2018. vegan: community ecology package. R package version 2.5-1. https://cran.r-project.org/web/packages/vegan/index.html. Accessed 11 Nov 2018.

Ozaki, K., M. Isono, T. Kawahara, S. Iida, T. Kudo, and K. Fukuyama. 2006. A mechanistic approach to evaluation of umbrella species as conservation surrogates. Conservation Biology 20:1507–1515.

Pike, D. A., J. K. Webb, and R. Shine. 2011. Removing forest canopy cover restores a reptile assemblage. Ecological Applications 21: 274–280.

Pilliod, D. S., and J. L. Welty. 2013. Land Treatment Digital Library: U.S. Geological Survey Data Series 806. http://pubs.er.usgs.gov/publication/ds806. Accessed 6 Dec 2018.

Pilliod, D. S., J. L. Welty, and G. R. Toevs. 2017. Seventy-five years of vegetation treatments on public rangelands in the great basin of North America. Rangelands 39(1):1–9.

Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344:1246752.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reynolds, T. D. 1979. Response of reptile populations to different land management practices on the Idaho National Engineering Laboratory site. Great Basin Naturalist 39:255–262.

Reynolds, T. D., and C. H. Trost. 1980. The response of native vertebrate populations to crested wheatgrass planting and grazing by sheep. Journal of Range Management 33:122–125.

Ricotta, C., and J. Podani. 2017. On some properties of the Bray-Curtis dissimilarity and their ecological meaning. Ecological Complexity 31:201–205.

Rieder, J. P., T. A. S. Newbold, and S. M. Ostoja. 2010. Structural changes in vegetation coincident with annual grass invasion negatively impacts sprint velocity of small vertebrates. Biological Invasions 12:2429–2439.

Roberge, J.-M., and P. Angelstam. 2004. Usefulness of the umbrella species concept as a conservation tool. Conservation Biology 18:76–85.

Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biological Conservation 129:323–335.

Runge, C. A., J. C. Withey, D. E. Naugle, J. E. Fargione, K. J. Helmstedt, and A. E. Larsen. 2019. Single species conservation as an umbrella for management of landscape threats. PLoS ONE 14(1):e0209619.

Sands, A. R., S. Sather-Blair, and V. Saab. 1999. Sagebrush steppe wildlife: historical and current perspectives. Pages 27–35 *in* P. G. Entwistle, A. M. DeBolt, J. H. Kaltenecker, and K. Steenhof, compilers. Proceedings of the Sagebrush Steppe Ecosystems Symposium. Bureau of Land Management, Boise, Idaho, USA.

Shinneman, D. J. 2019. North American sagebrush steppe and shrubland. Reference Module in Earth Systems and Environmental Sciences. https://doi.org/10.1016/B978-0-12-409548-9.11982-7

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biological Conservation 83:247–257.

Stiver, S. J., A. D. Apa, J. R. Bohne, S. D. Bunnell, P. A. Deibert, S. C. Gardner, M. A. Hilliard, C. W. McCarthy, and M. A. Schroeder. 2006. Greater Sage-grouse Comprehensive Conservation Strategy. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

U.S. Department of Agriculture. 2015. Outcomes in Conservation: Sage Grouse Initiative. Progress Report. National Resources Conservation Service, Washington, D.C., USA.

U.S. Fish and Wildlife Service [USFWS]. 2013. Greater Sage-grouse (*Centrocercus urophasianus*) conservation objectives: Final report. U.S. Fish and Wildlife Service, Denver, Colorado, USA.

U.S. Fish and Wildlife Service [USFWS]. 2014. Conservation Efforts Database. U.S. Department of the Interior. <www.conservationefforts.org>. Accessed 26 Sep 2018.

U.S. Geological Survey [USGS]. 2018. U.S. Geological Survey—Gap Analysis Project Species Habitat Maps CONUS_2001. U.S. Geological Survey data release, https://doi.org/10.5066/F7V122T2. http://gapanalysis.usgs.gov. Accessed 1 Aug 2018.

Werschkul, D. F. 1982. Species-habitat relationships in an Oregon cold desert lizard community. Great Basin Naturalist 380–384.

West, N. E., and J. A. Young. 2000. Vegetation of Intermountain valleys and lower mountain slopes. Pages 255–284 *in* M. A. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Second edition. Cambridge University Press, New York, New York, USA.

Wilcox, B. A. 1984. In situ conservation of genetic resources: Determinants of minimum area requirements. Pages 18–30 *in* J. A. McNeely and K. R. Miller, editors. National Parks, conservation and development: the role of protected areas in sustaining society. Proceedings of the World Congress on National Parks. Smithsonian Institution Press, Washington, D.C., USA.

Zipkin, E. F., J. A. Royle, D. K. Dawson, and S. Bates. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. Biological Conservation 143:479–484.

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