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Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates

Mary M. Rowland[a,*], *Michael J. Wisdom*[a], *Lowell H. Suring*[b], *Cara W. Meinke*[c]

[a]*USDA Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850-3368, USA*

[b]*USDA Forest Service, Terrestrial Wildlife Ecology Unit, Forestry Sciences Laboratory, 316 E. Myrtle Street, Boise, ID 83702, USA*

[c]*USGS Biological Resources Discipline, Snake River Field Station, 970 Lusk Street, Boise, ID 83706, USA*

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A B S T R A C T

Widespread degradation of the sagebrush ecosystem in the western United States, including the invasion of cheatgrass, has prompted resource managers to consider a variety of approaches to restore and conserve habitats for sagebrush-associated species. One such approach involves the use of greater sage-grouse, a species of prominent conservation interest, as an umbrella species. This shortcut approach assumes that managing habitats to conserve sage-grouse will simultaneously benefit other species of conservation concern. The efficacy of using sage-grouse as an umbrella species for conservation management, however, has not been fully evaluated. We tested that concept by comparing: (1) commonality in land-cover associations, and (2) spatial overlap in habitats between sage-grouse and 39 other sagebrush-associated vertebrate species of conservation concern in the Great Basin ecoregion. Overlap in species' land-cover associations with those of sage-grouse, based on the φ (*phi*) correlation coefficient, was substantially greater for sagebrush obligates ($\bar{x} = 0.40$) than non-obligates ($\bar{x} = 0.21$). Spatial overlap between habitats of target species and those associated with sage-grouse was low (mean $\varphi = 0.23$), but somewhat greater for habitats at high risk of displacement by cheatgrass (mean $\varphi = 0.33$). Based on our criteria, management of sage-grouse habitats likely would offer relatively high conservation coverage for sagebrush obligates such as pygmy rabbit (mean $\varphi = 0.84$), but far less for other species we addressed, such as lark sparrow (mean $\varphi = 0.09$), largely due to lack of commonality in land-cover affinity and geographic ranges of these species and sage-grouse.

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1. Introduction

The extent and quality of the sagebrush (*Artemisia* spp.) ecosystem across western North America are declining dramatically (Knick, 1999; Miller and Eddleman, 2000; Bunting et al., 2002; Connelly et al., 2004). West (2000) estimated that 25% of the sagebrush ecosystem – which historically occupied >100 million ha but has contracted to approximately 43 million ha – has been overtaken by invasive non-native annual grasses such as cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusa*), resulting in large-scale ecological changes. Among the sagebrush regions most drastically altered is the Great Basin of the western USA (Fig. 1), which currently contains 20% of all sagebrush in North America (Knick et al., 2003). Moreover, 30% of the Great Basin is dominated by sagebrush, a higher percentage than any other ecoregion in

* *Corresponding author:* Tel.: +1 541 962 6582; fax: +1 541 962 6504.
E-mail addresses: mrowland@fs.fed.us (M.M. Rowland), mwisdom@fs.fed.us (M.J. Wisdom), lsuring@fs.fed.us (L.H. Suring), carawolffm@hotmail.com (C.W. Meinke).
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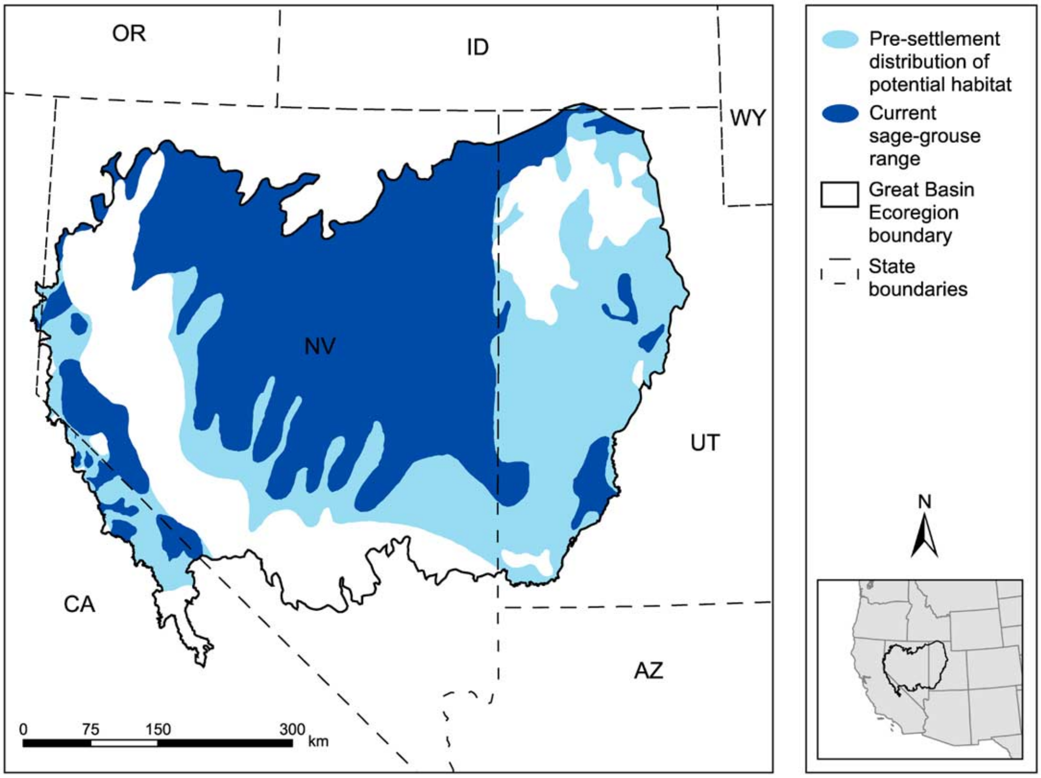

Fig. 1 – Location of the Great Basin ecoregion and pre-settlement distribution of potential habitat and current range of greater sage-grouse in the Great Basin (derived from Schroeder, 2002); pre-settlement distribution and current range combined comprise the historical range of sage-grouse used in analysis.

western North America except the Wyoming Basins (55%) and the Columbia Plateau (48%) (Wisdom et al., 2005). In the Great Basin, extensive, intense fires and the associated spread of cheatgrass have eliminated or altered millions of hectares of sagebrush and other arid shrublands (Bureau of Land Management, 1999; Nachlinger et al., 2001; Young and Sparks, 2002; Wisdom et al., 2005).

Concomitant with expanding interest in the sagebrush ecosystem has been interest in the fate of greater sage-grouse (*Centrocercus urophasianus*), a widespread species considered synonymous with the sagebrush ecosystem (Braun et al., 1976; Schroeder et al., 1999; Connelly et al., 2004). (Hereafter, sage-grouse refers to greater sage-grouse, not Gunnison sage-grouse (*C. minimus*).) A variety of land uses, such as grazing by domestic and feral livestock, conversion to agriculture, altered fire regimes, and energy development, have been implicated in declining habitats and populations of sage-grouse across the species' range (Schroeder et al., 1999, 2004; Connelly et al., 2004; Crawford et al., 2004). The range of greater sage-grouse has contracted 45% across North America (Schroeder et al., 2004) and 39% in the Great Basin (Fig. 1). These negative trends have spawned a plethora of efforts focused on sage-grouse populations and the maintenance and restoration of sagebrush communities (e.g. Bunting et al., 2002; Bureau of Land Management, 2004; Connelly et al., 2004). Greater sage-grouse was recently evaluated as a candidate for listing as threatened or endangered under the US Endangered Species Act (ESA, 1973), but was found not warranted for listing (U.S. Department of the Interior, 2005a). Despite this finding, sage-grouse remain a key focus of management in the sagebrush ecosystem (Bureau of Land Management, 2004). Other sagebrush-associated species, such as the pygmy rabbit (*Brachylagus idahoensis*), also are of concern (Knick et al., 2003; Dobkin and Sauder, 2004; Rich et al., 2005; U.S. Department of the Interior, 2005b).

Sage-grouse have been advanced as an indicator or umbrella species for other sagebrush-associated species and the sagebrush ecosystem (Dobkin, 1995; Rich and Altman, 2001; Rich et al., 2005). The umbrella species concept is used in conservation planning to protect biodiversity of typically lesser-known taxa (Simberloff, 1998; Caro and O'Doherty, 1999; Andelman and Fagan, 2000; Fleishman et al., 2000, 2001). Roberge and Angelstam (2004, 77) defined an umbrella species as one "whose conservation confers protection to a large number of naturally co-occurring species." The most common criterion in selecting an umbrella species is a broad geographic range, and thus presumed co-occurrence with a large number of other species (Fleury et al., 1998; Simberloff, 1998; Caro and O'Doherty, 1999; Andelman and Fagan, 2000). How well a species or group of species functions as an umbrella depends largely on the objective of the umbrella application. If the objective is to benefit multiple species through improvement of habitats for the umbrella species, criteria in addition to co-occurrence must be considered. First, resource requirements of the umbrella species must overlap with those of other targets of protection. Species with similar geographic distributions but dissimilar land-cover associations may not benefit from habitat management for the umbrella species. Second, management prescriptions appropriate for the umbrella species must also benefit other targeted species. Other criteria used to select umbrella species include a moderate level of prevalence and high sensitivity to human disturbance (Fleishman et al., 2000), sound knowledge of the species' biology and life history (Caro and O'Doherty, 1999), and legal protection (Rubinoff, 2001).

Based on these criteria, greater sage-grouse hold promise as an umbrella species because they are: (1) closely associated with sagebrush communities across their wide range, and thus co-occur with a host of other shrubland species (Paige and Ritter, 1999; Connelly et al., 2004; Rich et al., 2005); (2) currently neither rare nor ubiquitous (Connelly et al., 2004; Schroeder et al., 2004); (3) sensitive to anthropogenic disturbances (Lyon and Anderson, 2003; Aldridge, 2005); and (4) better-studied than most species associated with sagebrush (Rowland and Wisdom, 2002; Connelly et al., 2004). In addition, explicit guidelines for managing habitat for sage-grouse (Connelly et al., 2000) and monitoring their populations (Connelly et al., 2003) have been published.

In a recent assessment of habitat threats in the sagebrush ecosystem of the Great Basin, Rowland et al. (2005) evaluated the efficacy of sage-grouse as an umbrella species in relation to 39 other sagebrush-associated vertebrate species of concern. They did this by estimating the overlap in geographic ranges, habitat area, and habitat at risk to cheatgrass displacement of the 39 species with the current geographic range of sage-grouse. However, Rowland et al. (2005) calculated the area of habitat for each species that occurred within the current range of sage-grouse, without regard to whether areas mapped as habitat for target species coincided with habitat for sage-grouse. Consequently, their analysis provided a coarse-scale approximation of potential overlap in habitat area between sage-grouse and target species of concern, but did not explicitly evaluate the spatial overlap between land-cover types used as habitat by target species and greater sage-grouse. Rowland et al. (2005) also did not evaluate various ways in which habitat overlap can be assessed, such as considering areas mapped both as habitat and non-habitat.

To build upon and complement the preliminary work of Rowland et al. (2005), we compared similarities in land-cover associations and spatial overlap in habitats between sage-grouse and species of concern in the Great Basin, using a variety of metrics. The objectives of this complementary analysis were to: (1) determine the overlap in land-cover association (i.e., land-cover types used as habitat) between each species and sage-grouse; (2) determine the spatial overlap with sage-grouse of each species' habitat and their habitat at high risk of displacement by cheatgrass; and (3) discuss our results in the context of conservation planning.

2. Methods

2.1. The study area

We conducted our evaluation in the Great Basin ecoregion (hereafter referred to as the Great Basin) as defined by The Nature Conservancy (Nachlinger et al., 2001, Fig. 1). The Great Basin encompasses >29 million ha between the eastern flank of the Sierra Nevada Mountains in California and the Wasatch Mountains of central Utah. Vegetation is dominated by shrublands, with woody sagebrush species covering >30% (8.8 million ha) (Knick et al., 2003; Wisdom et al., 2005). Wyoming big sagebrush (*A. tridentata wyomingensis*) dominates sagebrush communities of the ecoregion; however, black sagebrush (*A. nova*), low sagebrush (*A. arbuscula*), and mountain big sagebrush (*A. t. vaseyana*) also are common. Federally managed lands comprise nearly 80% of the ecoregion, and 87% of the sagebrush in the Great Basin occurs on federal lands (Wisdom et al., 2005). Various salt desert shrub species, such as shadscale (*Atriplex confertifolia*) and fourwing saltbush (*A. canescens*), also compose a substantial fraction (29%) of the ecoregion (Wisdom et al., 2005). Major threats to native biodiversity and ecological processes in the Great Basin include invasions by exotic species and altered fire regimes (Young and Allen, 1997; Nachlinger et al., 2001; Wisdom et al., 2005).

2.2. Selection of species and land-cover associations

We evaluated sage-grouse as an umbrella species for 39 other sagebrush-associated vertebrates of conservation concern, all of which were included in a regional habitat assessment in the Great Basin (Wisdom et al., 2005). Species of concern were defined as those with declining or rare populations or habitats within the ecoregion, and were selected using a multi-step screening process (Wisdom et al., 2005). Criteria for selection included state-level ranks as applied by NatureServe (sensu Master, 1991; NatureServe, 2005) and association with macrohabitats that could be mapped accurately with the coarse-scale vegetation data available for our assessment. The 39 species included 1 amphibian, 9 reptiles, 16 birds (10 passerines, 6 raptors), and 13 mammals (Table 1).

To develop measures of overlap for our analyses, we used a land-cover classification of 90 m resolution developed explicitly for regional assessment of sagebrush communities (Comer et al., 2002). This coverage delineated 47 land-cover types in the Great Basin, based on the dominant overstory canopy species. Both to link species with land-cover and to quantify habitat in the Great Basin for species we evaluated, we constructed a land-cover association matrix using the cover types available in the land-cover map. (We define habitat in this paper as those land-cover types depicted in the Comer et al. (2002) coverage that are regularly occupied by a particular species.) Such matrices are the foundation for many habitat evaluations conducted at regional scales (e.g. Block et al., 1994; Johnson and O'Neil, 2001). Each species was associated with one or more of the land-cover types based on literature review (e.g., Maser et al., 1984) and consultation with species experts familiar with both the taxonomic group in question and the ecoregion (see Wisdom et al., 2005, for details).

2.3. Measures of overlap between species of concern and greater sage-grouse

We used the extent of overlap in three measures to evaluate the effectiveness of greater sage-grouse as an umbrella species in the Great Basin: (1) land-cover association, (2) habitat, and (3) habitat at high risk of displacement by cheatgrass. The

Table 1 – Sagebrush-associated species of conservation concern evaluated in the Great Basin ecoregion, in addition to greater sage-grouse (*Centrocercus urophasianus*)[a]

Species	Group association[b]
Herptiles	
Great Basin spadefoot *Spea intermontana*	Habitat generalist
Nightsnake *Hypsiglena torquata*	Habitat generalist
Striped whipsnake *Masticophis taeniatus*	Habitat generalist
Common sagebrush lizard *Sceloporus graciosus*	Sagebrush obligate[c]
Desert spiny lizard *Sceloporus magister*	Salt desert shrub
Long-nosed snake *Rhinocheilus lecontei*	Salt desert shrub
Groundsnake *Sonora semiannulata*	Salt desert shrub
Great Basin collared lizard *Crotaphytus bicinctores*	Salt desert shrub
Long-nosed leopard lizard *Gambelia wislizenii*	Salt desert shrub
Desert horned lizard *Phrynosoma platyrhinos*	Salt desert shrub
Raptors	
Ferruginous hawk *Buteo regalis*	Habitat generalist
Swainson's hawk *Buteo swainsoni*	Habitat generalist
Northern harrier *Circus cyaneus*	Shrubland
Prairie falcon *Falco mexicanus*	Shrubland
Short-eared owl *Asio flammeus*	Shrubland
Western burrowing owl *Athene cunicularia hypugaea*	Shrubland
Passerines	
Lark sparrow *Chondestes grammacus*	Habitat generalist
Brewer's blackbird *Euphagus cyanocephalus*	Habitat generalist
Vesper sparrow *Pooecetes gramineus*	Sagebrush "near-obligate"
Sage thrasher *Oreoscoptes montanus*	Sagebrush obligate
Sage sparrow *Amphispiza belli*	Sagebrush obligate
Brewer's sparrow *Spizella breweri*	Sagebrush obligate
Gray flycatcher *Empidonax wrightii*	Sagebrush-woodland
Green-tailed towhee *Pipilo chlorurus*	Sagebrush-woodland
Black-throated sparrow *Amphispiza bilineata*	Shrubland
Loggerhead shrike *Lanius ludovicianus*	Shrubland
Mammals	
Wyoming ground squirrel *Spermophilus elegans nevadensis*	Sagebrush "near-obligate"
Pygmy rabbit *Brachylagus idahoensis*	Sagebrush obligate
Pronghorn *Antilocapra americana*	Sagebrush obligate
Sagebrush vole *Lemmiscus curtatus*	Sagebrush obligate
Merriam's shrew *Sorex merriami*	Sagebrush-woodland
White-tailed jackrabbit *Lepus townsendii*	Sagebrush-woodland
Merriam's kangaroo rat *Dipodomys merriami*	Salt desert shrub
Chisel-toothed kangaroo rat *Dipodomys microps*	Salt desert shrub
Kit fox *Vulpes macrotis*	Shrubland
Ord's kangaroo rat *Dipodomys ordii*	Shrubland
Dark kangaroo mouse *Microdipodops megacephalus*	Shrubland
Little pocket mouse *Perognathus longimembris*	Shrubland
Northern grasshopper mouse *Onychomys leucogaster*	Shrubland

a Species selected for analysis were those identified by Wisdom et al. (2005) for regional assessment of species of concern in the sagebrush ecosystem of the Great Basin.
b Species were assigned to groups based on land-cover associations and habitat area in various land-cover types in the Great Basin (Wisdom et al., 2005).
c Sagebrush obligates were defined as species that are "restricted to sagebrush habitats during the breeding season or year-round" (Paige and Ritter, 1999, 5); sagebrush near-obligates occur in both sagebrush and other habitats, such as grasslands (Paige and Ritter, 1999). Sagebrush obligates and near-obligates were assigned to the sagebrush group.

first measure was not spatially based, but rather was a quantitative evaluation of the similarity between land-cover associations of sage-grouse and the target species. By contrast, the remaining two measures, habitat and habitat at risk, were spatially explicit evaluations of habitat overlap between sage-grouse and the target species.

To evaluate spatial overlap in habitat and habitat at risk, analyses were constrained within each species' geographic range in the Great Basin. For the 39 target species, current geographic range maps from standard sources (e.g. Rotenberry et al., 1999; Wilson and Ruff, 1999) were scanned and digitized (Wisdom et al., 2005). For greater sage-grouse, we used the species' historical range as depicted by Schroeder (2002, Fig. 1); this range covers 22.1 million ha (75%) of the ecoregion. We used the historical range of sage-grouse to emphasize the area in which vegetation manipulation, such as restoration of sagebrush communities, might be focused. We defined geographic range as the polygon or polygons that encompass the outer boundaries of a species' presence within the study area (i.e., "extent of occurrence", Gaston, 1991); this is not equivalent to a species' area of occupancy. Coarse-scale geographic range maps such as those used in our analyses commonly underpin conservation planning and assessment at regional scales (e.g. Knick et al., 2003; Marcot et al., 2003; Laliberte and Ripple, 2004).

To determine spatial overlap in habitat, we first mapped habitats for each species in a geographic information system (GIS) by selecting all land-cover types associated with the species within its geographic range in the Great Basin (Wisdom et al., 2005). We then overlaid the habitat maps for each species with that for sage-grouse and calculated overlap with the φ correlation coefficient, explained below.

To examine spatial overlap of habitat at risk of displacement by cheatgrass, we used a cheatgrass risk model previously developed and applied to habitats of each of the 39 target species and sage-grouse in the Great Basin. This rule-based model incorporates five variables: aspect, slope, elevation, landform, and ecological province (see Wisdom et al., 2005 for further details). Each 90 m pixel in the Great Basin was assigned to one of four cheatgrass risk categories: none, low, moderate, or high. For the analysis reported in this paper, we used only areas within the high-risk category. High-risk areas were defined as those where cheatgrass is likely to dominate the understory currently and with a high likelihood of displacement of native sagebrush or other native plant communities by cheatgrass within 30 years (Wisdom et al., 2005). We used the resulting maps of habitat at high risk for each species to compute overlap with habitat at risk for sage-grouse.

For all three measures, we calculated the φ correlation coefficient to provide estimates of overlap. The φ coefficient is a sample statistic used to assess the strength of association between two binary or dichotomous variables. Values of φ can range from -1 to 1; thus, the coefficient reveals not only the strength but also the direction of the association (Zar, 1998). A φ value near zero (approximately -0.3 to 0.3) suggests little or no monotonic relation between the two variables, whereas values >0.3 or <-0.3 indicate a positive or negative association, respectively. A large (e.g. >0.7) value of φ indicates a strong relation. Moreover, φ values account for overlap that might be expected from chance alone, as follows. If habitats for two species occur independently, then the chance of these habitats co-occurring is the product of their individual probabilities. (For example, if 60% of the area is habitat for species X and 40% for species Y, then 24% would be habitat for both.) In this case φ would equal zero; thus, departures of φ from zero indicate the relative gain (if $\varphi > 0$) or loss (if $\varphi < 0$) one would expect by focusing conservation efforts on the umbrella species, in our case greater sage-grouse, compared with non-target efforts.

Values of φ were calculated for each of four mutually exclusive combinations of two binary variables. For overlap in land-cover association, the four categories were: (1) cover-type used by species X but not by sage-grouse, (2) cover-type used by sage-grouse but not by species X, (3) cover-type used by both species, and (4) cover-type used by neither species. In calculating φ for spatial overlap in habitat and habitat at high risk, we considered the total area within each species' geographic range in the Great Basin, including non-habitat. The inclusion of non-habitat was required to calculate one of the four mutually exclusive categories mentioned above. In φ calculations for habitat overlap, information about areas not considered habitat for either sage-grouse or the target species was equally important as information about shared habitats. Thus, the four categories for habitat overlap were: (1) pixel mapped as habitat for species X but not sage-grouse; (2) pixel mapped as habitat for sage-grouse but not species X; (3) pixel mapped as habitat for both species (i.e. within the ranges and a land-cover-type considered habitat for both species); and (4) pixel not mapped as habitat for either species. For habitat and habitat at risk, the four combinations were spatially defined with a GIS (ARCINFO 8.3, ESRI, Redlands, CA) using a series of conditional statements in ARC Macro Language that were based on the selection criteria described above.

For one of our three measures, overlap in land-cover affinity, we also calculated percent overlap, as follows. First, for each species we identified the cover types shared by that species and sage-grouse, using the species-land-cover association matrices described above. We then divided the number of shared cover types by the total number of cover types used by each target species to derive a percentage.

2.4. *Estimating habitat managed under the sage-grouse umbrella*

To gain further insight into the potential benefits to other species by managing habitats for greater sage-grouse, we calculated the following index. For each species, we quantified the area of habitat within the historical range of greater sage-grouse and shared with sage-grouse (i.e. a cover-type associated with both species) and then divided this by the species' total habitat in the Great Basin. This proportion represented the potential benefit to each species from management of all habitat for greater sage-grouse within its historical range. We assumed that all sites mapped as habitat had an equal chance of being occupied.

3. Results

3.1. *Overlap in land-cover association*

Ten land-cover types in the Great Basin were identified as habitat for sage-grouse, eight of which were sagebrush types (Wisdom et al., 2005). Thus, the maximum number of cover types that a species could share with sage-grouse was 10. Overlap in cover-type association with sage-grouse, as measured by percentage of land-cover types in common, ranged from 8% (chisel-toothed kangaroo rat) to 70% (Wyoming ground squirrel, Table 2). (See Table 1 for scientific names of vertebrates included in our analysis.) Other species with relatively high percent overlap in cover-type association were pygmy rabbit (64%), Merriam's shrew (53%), and pronghorn (50%). Mean percent overlap in land-cover association across all 39 species was 32%. Overlap in cover-type association with sage-grouse as measured by φ ranged from -0.21 for chisel-toothed kangaroo rat to 0.68 for pygmy rabbit; six species had negative values of φ (Table 2).

Table 2 – Comparisons of overlap in land-cover types used as habitat (land-cover association) and spatial overlap in habitat and habitat at high risk of displacement by cheatgrass between 39 species of conservation concern and greater sage-grouse in the Great Basin ecoregion

Taxon/species	Land-cover association		Habitat	High-risk habitat
	% Overlap [a]	*Phi*	*Phi*	*Phi*
Herptiles				
Great Basin spadefoot	32 (10/31)	0.37	0.24	0.28
Great Basin collared lizard	13 (2/15)	−0.13	−0.38	−0.24
Long-nosed leopard lizard	19 (3/16)	−0.04	−0.29	−0.21
Desert horned lizard	19 (3/16)	−0.04	−0.28	−0.21
Common sagebrush lizard	31 (8/26)	0.26	0.16	0.13
Desert spiny lizard	19 (3/16)	−0.04	−0.29	−0.14
Nightsnake	29 (9/31)	0.26	0.24	0.28
Striped whipsnake	27 (9/33)	0.22	0.26	0.29
Long-nosed snake	26 (5/19)	0.10	−0.22	−0.09
Groundsnake	24 (4/17)	0.04	−0.24	−0.04
Mean (SD)	23.9 (6.2)	0.10 (0.17)	−0.08 (0.27)	0.01 (0.22)
Raptors				
Ferruginous hawk	27 (9/33)	0.22	0.28	0.33
Swainson's hawk	29 (10/35)	0.30	0.24	0.28
Northern harrier	33 (10/30)	0.39	0.38	0.35
Prairie falcon	33 (9/27)	0.34	0.40	0.36
Short-eared owl	33 (10/30)	0.39	0.38	0.35
Western burrowing owl	35 (10/29)	0.41	0.39	0.35
Mean (SD)	31.7 (3.0)	0.34 (0.07)	0.35 (0.07)	0.34 (0.03)
Passerines				
Gray flycatcher	26 (5/19)	0.10	0.38	0.68
Sage thrasher	29 (4/14)	0.12	0.57	0.72
Loggerhead shrike	25 (6/24)	0.09	−0.04	0.09
Sage sparrow	38 (6/16)	0.28	0.55	0.72
Black-throated sparrow	24 (4/17)	0.04	0.17	0.19
Lark sparrow	22 (6/27)	0.03	0.01	0.24
Green-tailed towhee	20 (4/20)	−0.03	0.32	0.59
Vesper sparrow	44 (8/18)	0.45	0.81	0.92
Brewer's sparrow	36 (8/22)	0.35	0.50	0.67
Brewer's blackbird	25 (3/12)	0.05	−0.13	−0.02
Mean (SD)	28.9 (7.8)	0.15 (0.16)	0.31 (0.31)	0.48 (0.32)
Mammals				
Merriam's shrew	53 (9/17)	0.58	0.70	0.92
Kit fox	46 (5/11)	0.33	0.21	0.21
Pronghorn	50 (9/18)	0.55	0.46	0.35
Wyoming ground squirrel	70 (7/10)	0.62	0.75	0.97
Merriam's kangaroo rat	24 (4/17)	0.04	−0.25	−0.06
Chisel-toothed kangaroo rat	8 (1/13)	−0.21	−0.35	−0.22
Ord's kangaroo rat	33 (9/27)	0.34	0.36	0.34
Dark kangaroo mouse	40 (6/15)	0.31	0.20	0.24
Little pocket mouse	32 (6/19)	0.21	0.12	0.16
Northern grasshopper mouse	35 (9/26)	0.36	0.43	0.36
Sagebrush vole	47 (9/19)	0.53	0.62	0.91
White-tailed jackrabbit	37 (10/27)	0.45	0.54	0.92
Pygmy rabbit	64 (9/14)	0.68	0.85	0.97
Mean (SD)	41.5 (16.4)	0.37 (0.25)	0.36 (0.36)	0.47 (0.42)
Grand mean (SD)	32.2 (12.7)	0.24 (0.22)	0.23 (0.34)	0.33 (0.36)

a Percent overlap in cover types used as habitat was calculated by dividing the number of land-cover types shared with sage-grouse by the total number of cover types used as habitat by a species. Values in parentheses are raw data, i.e. the numerator is the number of land-cover types in common and the denominator is the total number of land-cover types used as habitat by the species.

Among taxonomic groups, mammals had both the greatest percent overlap ($\bar{x} = 42\%$) and correlation (mean $\varphi = 0.37$) in cover-type association, whereas herptiles had the least ($\bar{x} = 24\%$, mean $\varphi = 0.10$, Table 2). Similar to herptiles, passerines demonstrated both relatively low overlap ($\bar{x} = 29\%$) and correlation (mean $\varphi = 0.15$) in cover-type association; values for raptors were intermediate between those for passerines and mammals (Table 2). Correlation in cover-type association for sagebrush obligates was positive (mean $\varphi = 0.40$) and substantially greater than that for non-obligates (mean $\varphi = 0.21$, Fig. 2). Mammals were the most variable among taxonomic groups with regard to measures of overlap in cover-type association (Table 2).

Comparisons between percent overlap and φ for individual species revealed some differences between the two methods. For example, black-throated sparrow, Brewer's blackbird, and Merriam's kangaroo rat had nearly 25% overlap in cover-type association with sage-grouse, but φ values for these three species approached zero (Table 2). The 14 species with the lowest percent overlap also had the lowest correlation in cover-type association.

3.2. Spatial overlap in habitat

Analysis of spatial overlap in habitats shared with sage-grouse, as estimated by φ, revealed that 18 species (46%) shared substantial habitat with sage-grouse (i.e. φ >0.30). This value was strongly positive ($\varphi \geqslant 0.70$) for four species, including three small mammals and vesper sparrow (Table 2). Species with the highest correlations were either sagebrush obligates, such as pygmy rabbit, or associated closely with sagebrush-woodland cover types, such as white-tailed jackrabbit. Correlation in habitat with sage-grouse was strongly negative (<−0.30) for only two species, Great Basin collared lizard and chisel-toothed kangaroo rat, but less than zero for 10 species. Such values indicate distinct spatial separation in habitat from sage-grouse (Table 2).

Correlation in habitat for herptiles with sage-grouse was generally negative (mean $\varphi = -0.08$) and far lower than that for other taxonomic groups. However, there were some exceptions: Great Basin spadefoot, nightsnake, and striped whipsnake had greater correlations than most herptiles, approaching the mean scores for the other taxonomic groups. The φ values for mammals and raptors were greater than those for passerines (Table 2). Sagebrush obligates demonstrated a strong positive association in habitat with sage-grouse compared to non-obligates (Fig. 2).

3.3. Overlap in habitat at risk of displacement by cheatgrass

Nineteen species (49%) showed a positive association ($\varphi > 0.30$) with sage-grouse in spatial overlap of habitat at high risk of displacement by cheatgrass. For eight species, this association was strongly positive (Table 2). Two species, Wyoming ground squirrel and pygmy rabbit, had nearly complete spatial overlap of their high-risk habitats with those of sage-grouse ($\varphi = 0.97$). Twenty species showed little or no association in high-risk habitats with sage-grouse. For the eight species that commonly use salt desert shrub communities in addition to sagebrush (Table 1), φ values were negative (Table 2).

Mean values of φ for high-risk habitats were positive for all taxonomic groups with the exception of herptiles, which showed no association (mean $\varphi = 0.01$). For sagebrush obligates, φ indicated a strong positive association in high-risk habitats with those of sage-grouse (mean $\varphi = 0.64$) compared to other species (mean $\varphi = 0.26$, Fig. 2). In summary, spatial overlap with sage-grouse in habitats at risk, as measured by φ, was generally greater, and for some species substantially greater, than for all habitats, indicating a disproportionate amount of high-risk habitat associated with sage-grouse compared to total habitat.

3.4. Benefits to target species from managing habitats for greater sage-grouse

Estimates of the proportion of habitat for each species of concern that could benefit from management of habitat for sage-grouse within its historical range varied from 0.87 for Wyoming ground squirrel to 0.03 for Merriam's kangaroo rat

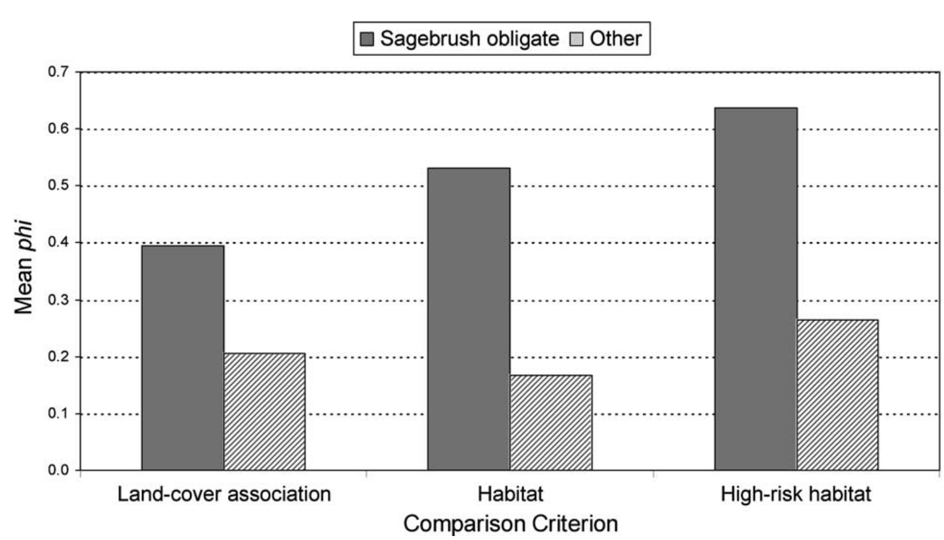

Fig. 2 – Overlap, based on the *phi* (φ) correlation coefficient, between greater sage-grouse and sagebrush obligates versus other species of conservation concern in the Great Basin for three criteria: land-cover association, habitat, and habitat at high risk of displacement from cheatgrass. Obligates included common sagebrush lizard, sage thrasher, sage sparrow, Brewer's sparrow, pronghorn, sagebrush vole, and pygmy rabbit.

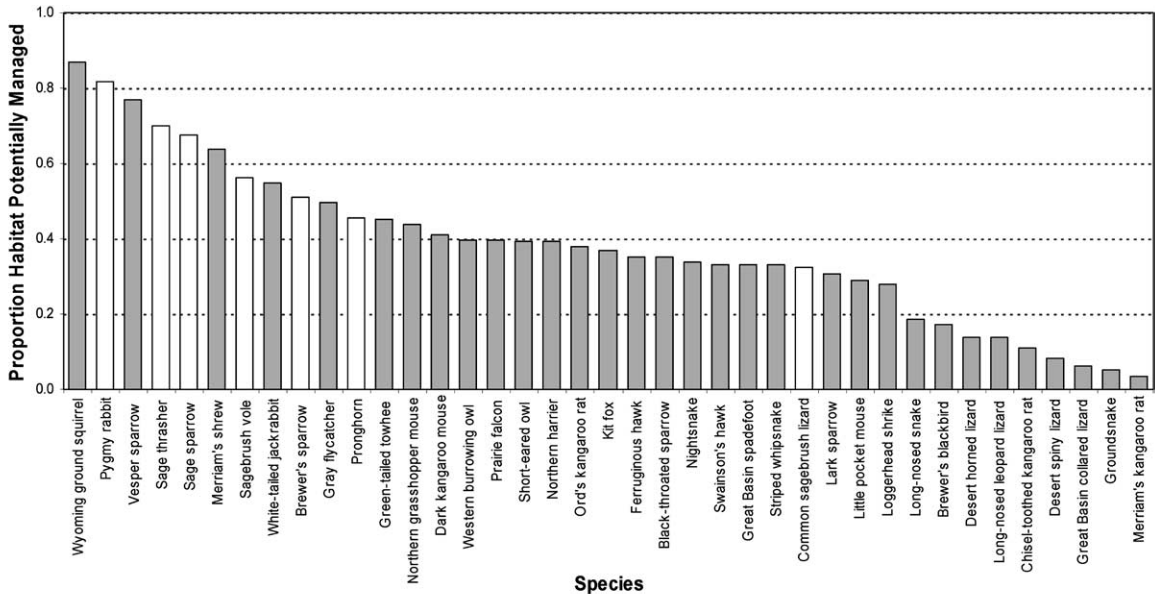

Fig. 3 – Estimated proportion of habitat for species of conservation concern in the Great Basin that would benefit from management of greater sage-grouse habitat within the historical range of sage-grouse in the Great Basin. Sagebrush obligate species are indicated by white bars.

(Fig. 3). Of the 10 species with at least half their habitat receiving potential benefits, five were sagebrush obligates (Fig. 3). The seven species with the least predicted benefit included five reptiles and the two kangaroo rat species.

4. Discussion

4.1. *Comparisons among species and cross-taxonomic coverage under the sage-grouse umbrella*

Based on our three coarse-filter measures of overlap, most sagebrush-associated species of concern in the Great Basin would benefit only marginally from conservation and restoration of sage-grouse habitats. Neutral values of φ (−0.3 to 0.3) for both habitat and high-risk habitat were found for about half the species in our assessment, indicating that management of sage-grouse habitat would confer no greater benefit than would management of randomly selected sites.

The use of φ statistics allowed a more spatially explicit evaluation of potential umbrella coverage by sage-grouse by accounting for co-occurrence of habitat for the target species and sage-grouse (cf. Rich et al., 2005; Rowland et al., 2005). For example, percent overlap in habitat area for long-nosed snake with the historical range of sage-grouse was 75% (unpublished data on file). Land-cover associations for this species were quite dissimilar from those of sage-grouse (Table 2), however, resulting in negative values of φ for habitat overlap.

Despite the generally poor performance of sage-grouse as an umbrella for most species in our study, some species, especially sagebrush obligates such as pygmy rabbit and Brewer's sparrow, may receive substantial conservation benefits if habitats for sage-grouse in the Great Basin are the focus of conservation planning and restoration. And for 18 species, including all sagebrush obligates except common sagebrush lizard, mean φ was >0.30, demonstrating a positive association with sage-grouse habitats (Fig. 4). The 18 species included 62% of the mammals and 50% of the passerines in our assessment, but none of the reptiles.

The relatively poor coverage by sage-grouse for many species is not surprising; evidence of cross-taxonomic protection with umbrella species is equivocal (Launer and Murphy, 1994; Fleury et al., 1998; Rubinoff, 2001; Fleishman et al., 2001; Betrus et al., 2005). Even among birds, sage-grouse was the only gallinaceous species we evaluated, and it differs substantially from other avian species we evaluated in life history characteristics such as body and home range size, diet, migratory status, and mating behavior. Even less is known about the potential overlap between environmental requirements for sage-grouse and those for herptiles and mammals associated with sagebrush cover types. Reptiles had uniformly low overlap in all criteria used in our evaluation; had we considered other environmental characteristics commonly associated with reptiles, such as presence of rocky outcrops, coverage by sage-grouse would likely have been even lower.

Recent research on wildlife in sagebrush landscapes has been predominantly focused on sage-grouse; however, many other species associated with sagebrush communities also are at risk (Knick et al., 2003; Dobkin and Sauder, 2004; Rich et al., 2005). Unfortunately, the Great Basin is among the ecoregions least consistently sampled for birds (Knick et al., 2003; Dobkin and Sauder, 2004) and other taxonomic groups such as herptiles (Setser et al., 2002). Sampling of small mammal populations in shrubsteppe communities in the western USA demonstrated that these species were often absent in presumably suitable habitats, and that current geographic range maps may grossly overestimate their distribution (Dobkin and Sauder, 2004).

The limited conservation umbrella of sage-grouse for many species in our assessment is related in part to the

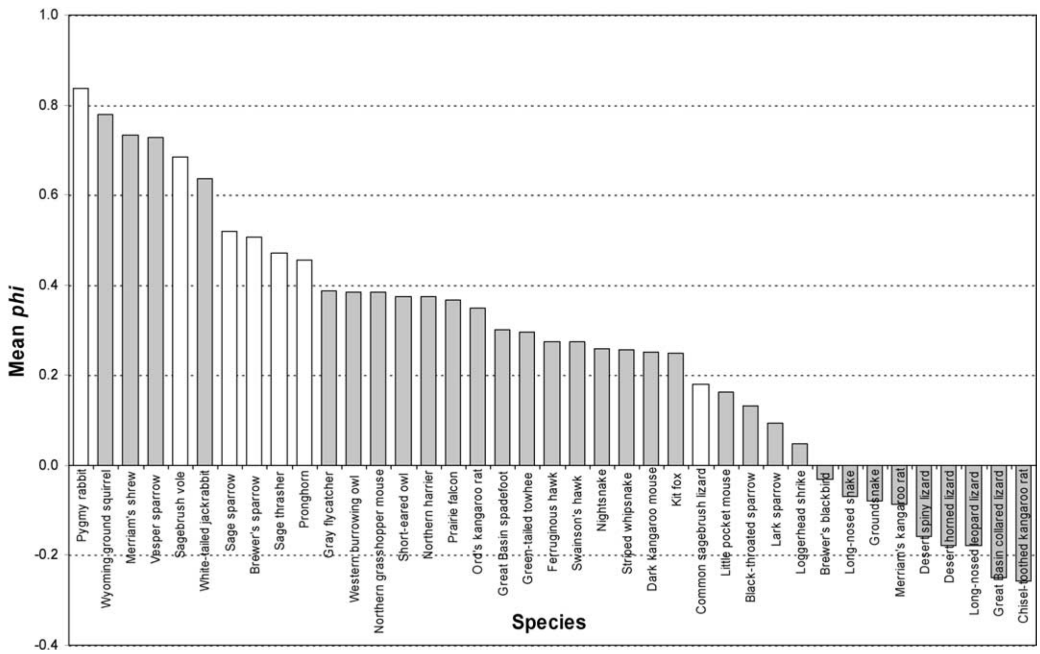

Fig. 4 – Mean *phi* (φ) for land-cover association, habitat, and habitat at high risk of displacement from cheatgrass, based on comparisons between greater sage-grouse and 39 species of conservation concern in the Great Basin. Sagebrush obligate species are indicated by white bars.

nearly complete reliance of sage-grouse on sagebrush; sage-grouse are among the few species identified as true "sagebrush obligates" (Schroeder et al., 1999). Although various authors have delineated sagebrush obligates and "near-obligates" (e.g. Braun et al., 1976; Paige and Ritter, 1999; McAdoo et al., 2004; Rich et al., 2005), many more non-obligate species are associated with sagebrush (McAdoo et al., 2004; Rich et al., 2005; Wisdom et al., 2005). For example, Dobkin and Sauder (2004, 1) identified 61 avian and small mammal species that are "completely or extensively dependent on shrubsteppe ecosystems in the Intermountain West." These species may depend on sagebrush communities during certain times of year, but also breed, forage, or disperse in other native shrubland, grassland, or woodland communities (McAdoo et al., 2004; Rich et al., 2005). Vegetation communities such as the salt desert shrub complex in the Great Basin, which comprised the most abundant habitat type for at least one-fourth the species in our assessment, are perhaps even more at risk than sagebrush, especially from invasion by non-native grasses (Svejcar and Tausch, 1991; Young and Sparks, 2002; Wisdom et al., 2005).

4.2. *Issues of scale*

Spatial and temporal scale, which we did not address in our evaluation, also may confound use of sage-grouse as an umbrella species for other vertebrates in the sagebrush ecosystem. In an evaluation of capercaillie (*Tetrao urogallus*) as an umbrella species for avian diversity in Central Europe, co-occurrence of capercaillie was greatest with non-passerines, and its spatial needs were considered far greater than most species in the assessment (Suter et al., 2002). Sage-grouse are considered a landscape-scale species (Connelly et al., 2004; Crawford et al., 2004), and home ranges for individual sage-grouse may vary from 100s to 1000s of hectares (Connelly et al., 2004; Rowland, 2004). By contrast, territories for many passerines, such as sage sparrows, are on the order of hectares (Martin and Carlson, 1998). With such large disparities in spatial extent of areas used by sage-grouse and less mobile species, particularly herptiles, declining trends in individual sage-grouse populations may not be apparent until other species associated with sagebrush communities have experienced far more severe population declines that may be difficult to reverse.

Moreover, little is known about differences in responses of sage-grouse versus other sagebrush-associated species to size and fragmentation of sagebrush patches (Crawford et al., 2004). Sage-grouse use a variety of patch sizes arranged in a mosaic across the landscape, a reflection of their high mobility and large home ranges (Connelly et al., 2004; Crawford et al., 2004). Sage sparrows, by contrast, appear to require large, unfragmented patches of sagebrush (Knick and Rotenberry, 1999), although these patches also may function as a mosaic at the scale at which they are used by sage sparrows. These disparities suggest that better knowledge is needed of the spatial characteristics of habitats of sage-grouse and other sagebrush fauna, particularly if sage-grouse are to be used as an umbrella species for vegetation management in sagebrush ecosystems.

4.3. *Potential benefits from habitat management for sage-grouse in the Great Basin*

For most species in our assessment, their geographic ranges overlap sufficiently with that of sage-grouse such that the majority of their habitat falls within the range of sage-grouse (Rich et al., 2005; Rowland et al., 2005). However, when the spatially explicit overlap in habitats for target species and sage-grouse was accounted for, only 10 of the 39 species had ⩾50% of their habitat both shared with sage-grouse and within the historical range of that species. Thus, conservation benefits to target species from habitat management applied to sage-grouse would be minimal for most species in our analysis.

Even within sagebrush communities in the range of sage-grouse, vegetation manipulation tailored to benefit sage-grouse may not improve habitat for other species. For example, management guidelines for sage-grouse emphasize the importance of maintaining a diverse grass and forb understory, with cover ⩾25% in breeding habitats (Connelly et al., 2000). But for other sagebrush obligates, such as Brewer's sparrow, an herbaceous understory with these characteristics may not be required or even desirable (Rotenberry et al., 1999). Moreover, selection for specific structural characteristics of sagebrush, such as shrub canopy cover, density, and height, may differ between sage-grouse and other sagebrush-associated species (e.g., Martin and Carlson, 1998; Rowland, 2004).

4.4. *Caveats and limitations of our analyses*

Several assumptions and limitations of our evaluation of sage-grouse as an umbrella species should be noted. First, we used geographic range maps to spatially constrain our estimates of potential habitat for species in our study, but recognize that some unknown portion of each species' range is unoccupied (Brown et al., 1996; Marcot et al., 2003). Co-occurrence of habitats occupied by individual target species and sage-grouse may be less or more than our estimates. In addition, our assumption that sagebrush habitats within the entire historical range of sage-grouse in the Great Basin will be the focus of conservation planning and active restoration is likely unrealistic. A more pragmatic scenario is that management will be constrained within the species' current range, which is a far smaller percentage (45%) of the ecoregion than its historical range. Conservation benefits to target species would be largely reduced under this scenario.

Second, we used maps of the current geographic range of target species in our analysis, in contrast with the use of the historical range of sage-grouse. This decision was driven by: (1) the widespread extirpation of sage-grouse populations across the species' range, resulting in an estimated range contraction of 45% (Schroeder et al., 2004), and (2) the focus of land and wildlife management agencies on evaluation of environmental conditions within, and potential restoration of, sagebrush communities at this larger spatial extent. Had we used historical range maps for the 39 target species in our analyses, estimates of spatial overlap in habitat and habitat at risk with sage-grouse would have been greater. For most of the 39 target species in the Great Basin, however, documented range contractions are rare, except for a handful of taxa, such as pronghorn (Laliberte and Ripple, 2004).

Third, although various land-cover types were designated as habitat for our species-land-cover association matrix, knowledge is lacking about the relative importance of these vegetation types for many species, particularly in terms of their potential role as source habitat (sensu Pulliam, 1988). Lacking this information, we did not weight cover types assigned to each species. Last, we quantified habitat according to the dominant overstory cover types in the sagebrush coverage (Comer et al., 2002). We assumed that vertebrates associated with the same cover types as sage-grouse had complete habitat overlap within those types. We did not consider finer-scale biotic or abiotic features such as presence of friable soils, an important feature for pygmy rabbit to establish and maintain burrows in sagebrush communities (e.g. Gabler et al., 2000), or understory characteristics. Had such data (i.e. more fine-scale habitat models and associated spatial data layers) been available for all target species across their ranges in the Great Basin, our estimates of overlap between target species and sage-grouse would have been lower than those resulting from our use of land-cover types alone.

5. Conclusions

Little empirical evidence exists for the utility of single-species approaches, whether umbrellas, indicators, or other shortcuts, in conservation planning (Niemi et al., 1997; Simberloff, 1998; Andelman and Fagan, 2000). In some cases, even randomly selected species performed at least as well as putative umbrella species in protecting other taxa (Andelman and Fagan, 2000; Fleishman et al., 2001; Bonn et al., 2002). We concur with others (e.g. Launer and Murphy, 1994; Fleishman et al., 2001; Roberge and Angelstam, 2004; Maes and Van Dyck, 2005) that a more fruitful approach may be the selection of a suite of umbrella species or establishment of species groups (Wisdom et al., 2005). For the sagebrush ecosystem, such a suite would include not only greater sage-grouse and other sagebrush obligates but also species closely associated with other plant communities adjacent to or embedded within the sagebrush matrix, such as native perennial grasslands or salt desert shrub. For example, Wisdom et al. (2005) placed sage-grouse and the 39 species we evaluated in five groups, each of which differed in their land-cover associations, habitat area, and habitat at risk in the Great Basin.

Alternative, coarse-filter management strategies may also be more effective in protecting the sagebrush ecosystem than the use of umbrella species. Coarse-filter management assumes that by maintaining representative land areas and habitats, the needs of all associated species will be met (Hunter, 1991; Marcot et al., 1994). Rigorous validation of this assumption is required, however, just as would be required of assumptions related to implementation of umbrella species or other single-species or grouping approaches.

If the umbrella approach is used, selected species should meet the general criteria of umbrellas (e.g. be wide-ranging and neither too rare nor too prevalent), without regard to population status. By using a previously developed index (Fleishman et al., 2000, 2001) to select umbrella species, important life history characteristics such as sensitivity to disturbance would be considered in tandem with measures of species co-occurrence and relative rarity.

Most umbrella species are selected retrospectively, rather than prospectively, typically in response to documented population declines or to potential listing as threatened or endangered (Fleishman et al., 2001). Sage-grouse are no exception, and join other species at risk that have been evaluated as umbrellas, such as the Alcon Blue butterfly in Belgium (*Macu-*

linea alcon, Maes and Van Dyck, 2005) and the California gnatcatcher (*Polioptila californica*, Fleury et al., 1998; Rubinoff, 2001). While threatened or endemic species may be legitimate conservation targets, their protection does not guarantee protection of biodiversity, even of similar taxa. In evaluating avian conservation in South Africa and Lesotho, Bonn et al. (2002) found that reserve networks designed to conserve threatened and endemic species may be inadequate in preserving overall biodiversity, especially locations in which other, non-target species were locally abundant.

Better empirical data are needed to document co-occurrence of sage-grouse and other species at finer spatial resolutions than used in our analyses. Rich et al. (2005) evaluated co-occurrence of sage-grouse and other sagebrush-associated bird species in the western USA, based on Breeding Bird Survey route data. They found significant correlations for 10 species, all of which were on our list except rock wren (*Salpinctes obsoletus*) and western meadowlark (*Sturnella neglecta*). This survey method, however, is not well-suited for monitoring sage-grouse presence, abundance, or trends (Connelly et al., 2004; Rich et al., 2005). A better approach may be to conduct extensive sampling, using appropriate methodology, for both vertebrates and invertebrates in sites known to be occupied by sage-grouse, as well as in sagebrush communities where sage-grouse have been extirpated. By combining these results with existing data on species distributions (e.g. through state Natural Heritage databases), one could more accurately assess the value of sage-grouse as an umbrella species. Furthermore, maps of biodiversity of species of concern throughout the sagebrush ecosystem could be generated and subsequently overlaid with maps of sage-grouse distribution. These overlays could be used in conservation planning to target habitat management and conservation for sage-grouse in sites with the greatest potential to benefit multiple species.

Ultimately, the effectiveness of sage-grouse as an umbrella species will depend on management objectives that identify the level of conservation coverage sufficient for the target species. Thus, specific objectives for invoking sage-grouse, or any other species, as an umbrella in conservation planning must be explicitly stated before the effectiveness of such an approach can be evaluated. Federal land management agencies such as the Bureau of Land Management and US Forest Service are required by law to manage for biodiversity and ecosystem health. Given that mandate, environmental conditions for all species of concern or special interest, not only sage-grouse, must be evaluated in land-use planning within sagebrush communities.

Based on our evaluation, sage-grouse may offer substantial conservation coverage for sagebrush obligates and "near-obligates." However, for the remaining taxa, management directed explicitly toward sage-grouse will provide few benefits. Although the sagebrush portion of habitats for all of the 39 species of concern within the range of sage-grouse, which for some species is significant, will likely benefit from improvements to sage-grouse habitat, this area represents a small percentage of total habitat for most species in the Great Basin.

Our regional-scale work highlights the need for conservation planners to explicitly consider the spatial overlap between sagebrush landscapes and particular land-cover types used by sage-grouse and by other species of concern to better understand what benefits will be gained by management targeted solely for sage-grouse. Equally important, such spatial analysis will highlight habitats for species of concern, especially those threatened by cheatgrass or other stressors, which will not be addressed through management for sage-grouse.

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