Research Reports

Greater sage-grouse of Grand Teton National Park: Where do they roam?

BRYAN BEDROSIAN, CRAIGHEAD BERINGIA SOUTH

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Figure 1. Male greater sage-grouse in flight during winter.

IN GENERAL, SPECIES ARE LOCATED WITHIN A BROADLY defined range, but they use only specific habitats within their range, often seasonally. For example, in a field guide to birds you will often see a map showing seasonal ranges and migration areas with text describing which areas, such as wetlands, are most used within the range. Recent research maps historical and current greater sage-grouse (*Centrocercus urophasianus*; fig. 1; hereafter sage-grouse) range, which has been reduced about 50% since European settlement (Schroeder et al. 2004). The loss of sagebrush (*Artemisia* spp.) habitat is the main cause of the current decline in sage-grouse, and the sage-grouse was recently found "warranted but precluded" for listing as endangered under the Endangered Species Act (U.S. Fish and Wildlife Service 2010). Natural resource managers need to understand how sage-grouse populations use existing habitat to persist so that landscapes can be managed to prevent the listing of the species as endangered.

Studies that have used landscape-scale, spatial approaches to examine sage-grouse habitat selection (Homer et al. 1993; Aldridge and Boyce 2007; Moynahan et al. 2007; Carpenter et al. 2010) generally confirm the importance of well-developed sagebrush stands. Within sagebrush habitat, however, sage-grouse further refine their habitat selection. In general, studies show that relative to random sagebrush locations, sage-grouse select habitats with

Abstract

Greater sage-grouse (*Centrocercus urophasianus*) population declines may be caused by range-wide degradation of sagebrush (woody *Artemisia* spp.) steppe ecosystems. Understanding how greater sage-grouse use the landscape is essential for successful management. We assessed greater sage-grouse habitat selection on a landscape level in Jackson Hole, Wyoming. We used a Geographic Information System (GIS) and radio-collared sage-grouse to compare habitat used and the total available landscape. Greater sage-grouse selected mountain big sagebrush (*A. tridentata* var. *vaseyana*) communities or mixed mountain big sagebrush–antelope bitterbrush (*Purshia tridentata*) communities and avoided low-sagebrush (*A. arbuscula*) dwarf shrubland. In spring and summer, sage-grouse primarily used sagebrush-dominated habitats on the valley floor and did not concentrate in mesic areas later in the summer as is typical of the species. The diversity of habitats used in winter exceeds that reported in the literature. In winter, Jackson Hole greater sage-grouse moved to hills, where they used various communities in proportion to their availability, including tall deciduous shrublands, cottonwood (*Populus angustifolia*) stands, exposed hillsides, and aspen (*P. tremuloides*) stands. Because seasonal habitat selection is not necessarily consistent across populations residing in different landscapes, habitat management should be specific to each population and landscape. This sage-grouse population provides an example that may offer insight into other species with seasonal habitat needs.

Key words: *Centrocercus urophasianus*, Grand Teton National Park, greater sage-grouse, Greater Yellowstone Ecosystem, habitat selection, sagebrush

greater sagebrush height and cover (Crawford et al. 2004; Hagen et al. 2007). In winter, sage-grouse prefer sagebrush exposed approximately 25–35 centimeters (9.8–13.8 in) above snow, often on south- and west-facing slopes (Connelly et al. 2000; Crawford et al. 2004; Hagen et al. 2007). For nesting and early brood-rearing, sage-grouse prefer relatively tall (40–80 cm or 15.7–31.5 in) sagebrush of moderate to high canopy cover (15–25%) with a well-developed grass and forb understory (Connelly et al. 2000; Hagen et al. 2007). As forbs dry through the summer, female sage-grouse and their broods are found in increasingly moist and even riparian habitats (Wallestad 1971). During nesting and brood-rearing, sage-grouse avoid cropland, oil wells, other anthropogenic habitats, badland-type habitats, loamy upland sites, and habitat edges, but select habitats with a rich grass component (Aldridge and Boyce 2007; Moynahan et al. 2007).

In Wyoming, an area with relatively intact sagebrush habitat, male breeding-ground attendance dropped 50% from 1965 to 2003 (Connelly et al. 2004). Population declines in areas with intact habitats suggest that degradation of remaining habitats may be an important cause of sage-grouse population declines (Braun 1998; Connelly et al. 2000). The Jackson Hole, Wyoming, sage-grouse provide a unique opportunity to study a population that exists in a complex landscape with much less homogenous sagebrush than is typically found in areas occupied by sage-grouse, and which may be limited by winter habitat availability (USRBSGWG 2008). Our work provides an example of how habitat use can be studied to describe fine-scale, individual, seasonal selection within a larger landscape—whether for other sage-grouse populations or other species. This type of information may be used by natural resource managers to conserve critical habitats such as winter habitat.

The Jackson Hole, Wyoming, sage-grouse provide a unique opportunity to study a population that exists in a complex landscape with much less homogenous sagebrush than is typically found in areas occupied by sage-grouse, and which may be limited by winter habitat availability.

We investigated three main questions about sage-grouse habitat use across the Jackson Hole area: (1) which habitats do sage-grouse use? (2) how does habitat selection vary seasonally? and (3) how does habitat selection in a complex landscape differ from selection in sagebrush-dominated landscapes more typical of the species?

Methods

We assessed landscape-level, sage-grouse habitat selection (Manly et al. 2002; Calenge and Dufour 2006) in and around Grand Teton National Park, Wyoming (1,255 sq km or 484 sq mi, 44° N, 110° W), within the Greater Yellowstone Ecosystem (Marston and Anderson 1991) using radiotelemetry data (Holloran and Anderson 2004). The many available habitats in the topographically complex landscape (e.g., elevation ranges from the 2,070-meter [6,792 ft] Snake River valley to the 4,197-meter [13,770 ft] summit of the Grand Teton) used by the Jackson Hole sage-grouse population allowed us to observe whether sage-grouse would use habitat not widespread in the species' typical, more homogenous sagebrush range. The analyses we employed have been used on a variety of

Table 1. Habitat classifications used in habitat selection analyses for greater sage-grouse in and surrounding Grand Teton National Park, Wyoming, 1999–2003

Habitat[a]	Description	% Study Area[b]	% Home Range[c]
Low sagebrush	*Artemisia arbuscula* dwarf shrubland	0.5	0.2
Mixed sagebrush–shrubby cinquefoil	*Artemisia* spp.–*Dasiphora fruticosa* mesic shrubland	1.1	0.8
Mixed big sagebrush–bitterbrush	*Artemisia tridentata–Purshia tridentata* mixed shrubland; sagebrush is predominantly mountain big sagebrush (*A. tridentata* ssp. vaseyana)	1.6	14.2
Big sagebrush	Artemisia tridentata dry shrubland; sagebrush is predominantly mountain big sagebrush (*A. tridentata* ssp. *vaseyana*)	10.8	58.5
Conifer forests	*Abies lasiocarpa–Picea engelmannii*, *Picea pungens*, *Pinus contorta*, and *Pseudotsuga menziesii* forests	33.9	0.9
Forb	Montane xeric and mesic forb herbaceous vegetation	3.2	1.5
Low hillside vegetation	Exposed hillside sparse vegetation	0.7	0.9
Disturbed	Human disturbed: canals, mixed urban, mineral extraction, and transportation	1.0	2.5
Grassland	Mixed herbaceous grassland	4.7	6.7
Cottonwood	*Populus angustifolia–P. balsamifera* riparian forest	1.0	3.6
Aspen	*Populus tremuloides* forest and woodland regeneration	2.6	2.6
Riparian	Lake shoreline, flooded wet meadow, *Salix* spp. shrubland, sand areas, stream deposits, and streams	5.7	3.7
Deciduous shrub	Mixed tall deciduous shrubland	1.3	3.1
Other	Habitat classes lacking sage-grouse relocations; e.g., alpine and subalpine vegetation, cliff, talus, and agricultural land	31.8	0.7

Notes: Habitat classifications are based on the Grand Teton National Park Vegetation Map (Cogan et al. 2005).

[a]Habitat names are as used in text and figures.

[b]Study area percentages are of the area covered by the Grand Teton National Park Vegetation Map (Cogan et al. 2005), which includes the park and surrounding areas.

[c]Home range percentages are of combined winter and summer 85% probability home ranges.

wildlife species (Johnson 1980; Manly et al. 2002; Alldredge and Griswold 2006), but rarely on sage-grouse.

Four main sagebrush communities available to this sage-grouse population were mountain big sagebrush (*A. tridentata* var. *vaseyana*) shrubland, low-sagebrush (*A. arbuscula*) dwarf shrubland, mixed mountain big sagebrush–antelope bitterbrush (*Purshia tridentata*) shrubland, and mixed sagebrush–shrubby cinquefoil (*Dasiphora fruticosa*) (table 1). Other shrubs present at varied densities throughout sagebrush communities included yellow and rubber rabbitbrush (*Chrysothamnus viscidiflorus* and *Ericameria nauseosa*) and snowberry (*Symphoricarpos* spp.). Cottonwoods (*Populus* spp.) occurred along riparian areas. At higher elevations, aspen (*Populus tremuloides*) woodlands occupied mesic, north-facing hollows, and mixed conifer forests (e.g., *Pinus contorta*, *Pinus flexilis*, *Picea engelmannii*, *Pseudotsuga menziesii*, *Abies lasiocarpa*) populated the hills and mountains (table 1).

We captured 15 male and 20 female sage-grouse at or near breeding grounds (leks) from mid-March through April 1999–2002 and fitted them with ≤25-gram (0.9 oz) radio transmitter necklaces (19% of the estimated population during 1999–2003; Advanced Telemetry Systems Inc., Isanti, Minnesota). We used the radio-collar data collected from 1999 to 2003 (Holloran and Anderson 2004; fig. 2) and Wyoming Game and Fish Department visual observation records from 1978 to 2006 to examine habitat use defined by observed sage-grouse locations.

In 2005 the U.S. Geological Survey and the National Park Service completed a digital vegetation map for Grand Teton National Park, John D. Rockefeller, Jr. Memorial Parkway, and surrounding areas (hereafter "the study area"; fig. 2; Cogan et al. 2005). The map covers 222,612 hectares (550,074 ac), with a mean polygon size of 7 hectares (17.3 ac) and a minimum effective unit of 0.5 hectare (1.2 ac). It has 52 land classes, 42 of which are vegetation types. We divided the land classes into 14 habitat groups based on ecological and structural similarity (table 1). To compare abiotic variables across habitats, we extracted data, including elevation and slope, from 1,747 field plots used to build and assess the map (Cogan et al. 2005).

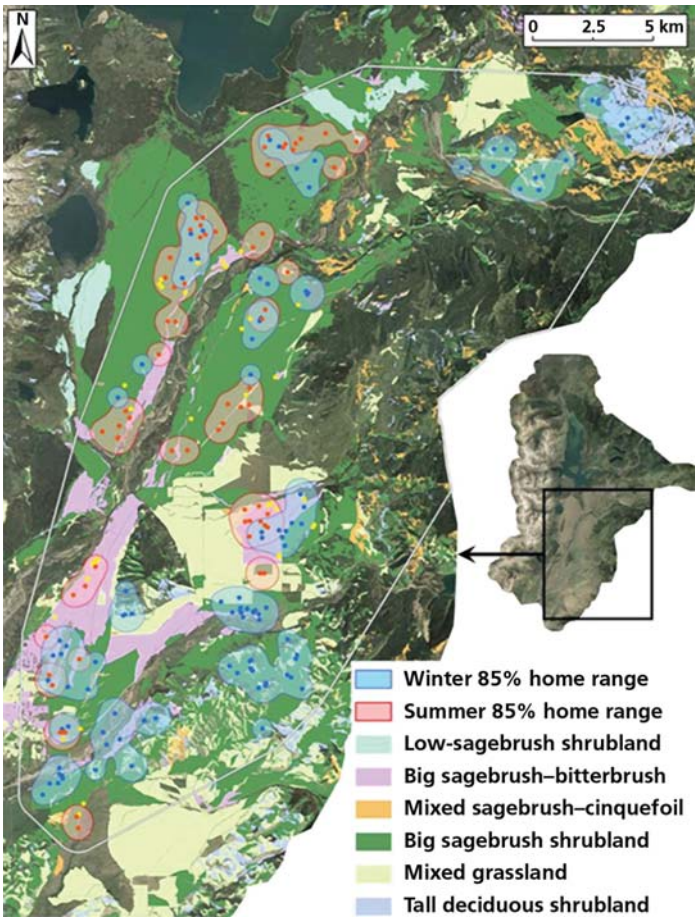


Figure 2. Orthophotos of Grand Teton National Park, Wyoming, including select vegetation types from the Grand Teton National Park Vegetation Map (Cogan et al. 2005) and sage-grouse relocation points from 1999–2003 (Holloran and Anderson 2004). Inset photo is of the entire study area (Grand Teton National Park Vegetation Map coverage area). Main image is Jackson Hole, Wyoming, the area used by greater sage-grouse. Red points are summer relocations, blue points are winter relocations, and yellow points are nest locations.

We used individual bird locations (n = 35 birds) to ask: (1) does each bird use the same habitat? and (2) do birds use habitat in proportion to its availability (Manly et al. 2002: 50; Calenge and Dufour 2006)? If each bird used different habitat, we would not be able to generalize their preferences, and if all habitats were used equally in proportion to their availability, we would not be able to identify preferred or critical habitats. Because of our small number of collared birds, we were conservative when deciding the significance of our findings (Cherry 1996; Payton et al. 2003), so our findings are robust.

We defined habitat use in two ways: (1) a bird uses the habitat class that encloses a radio-collar relocation point; and (2) a bird uses all classes within a 200-meter (656 ft) radius buffer of a relocation point proportionally to the area of the classes within the circle. The buffer definition of resource use emphasizes the importance of habitat mosaics and acknowledges that animals may select one habitat type because it is adjacent to another (Dickson and Beier 2002). We compared habitat use by each individual with habitat we defined to be available to the entire population (design 2; Thomas and Taylor 1990, 2006). Defining availability on the population level made biological sense because sage-grouse are gregarious and not territorial (Crawford et al. 2004).

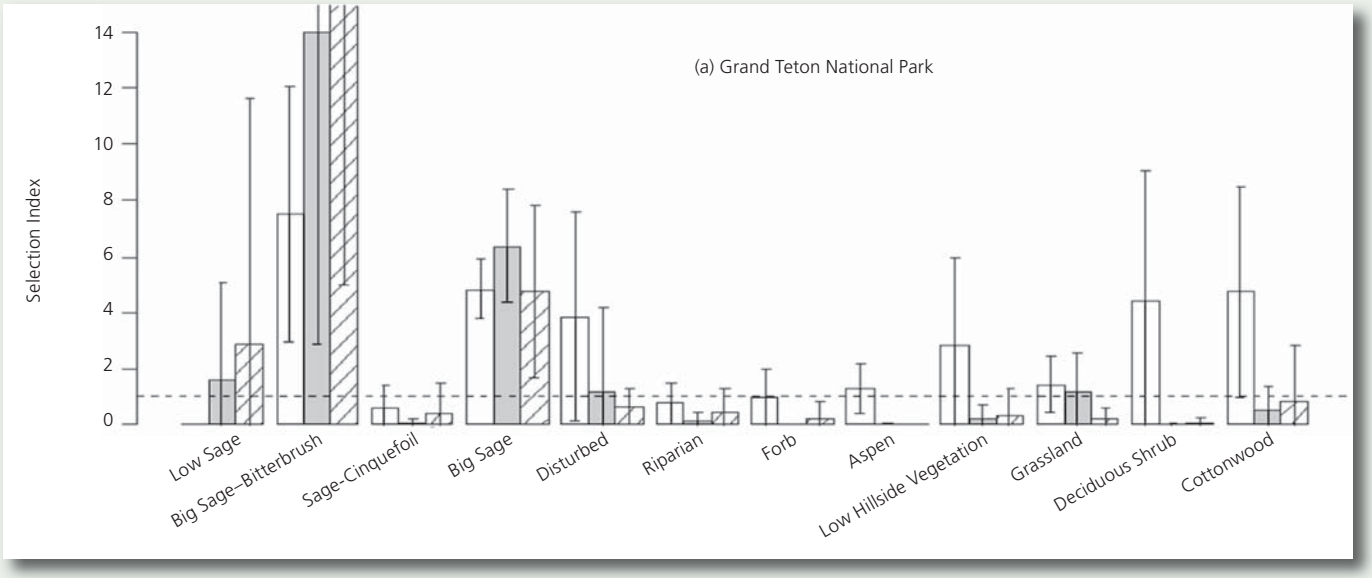
We used the R statistical programming language (R Project 2007) for statistical analyses and graphing. Package Adehabitat (Calenge 2006) and its supporting package Ade4 (Chessel et al. 2004) provided functions for compositional analysis, selection ratio analyses, and eigenanalysis (Calenge and Dufour 2006). We used ArcMap™ (ESRI 2006) with Spatial Analyst Tools and Hawth's Analysis Tools (Beyer 2007) for spatial calculations and analyses.

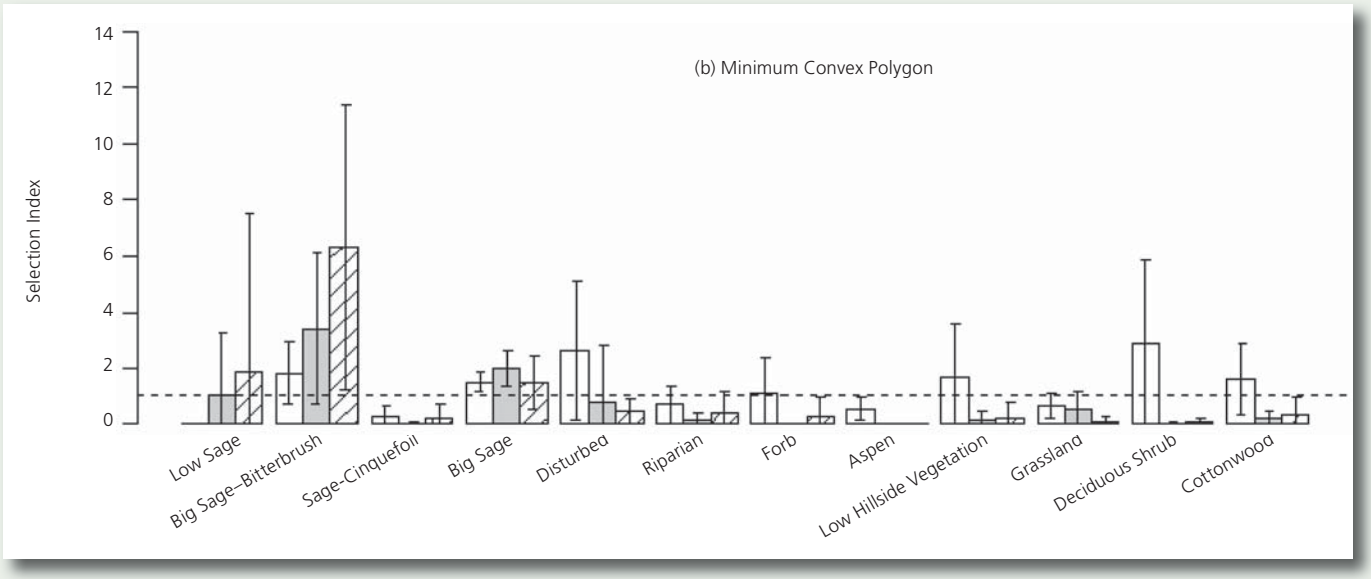
Results

As expected, chi-square statistical tests supported the hypothesis that individual collared birds used habitat the same way as all the other collared birds, so we can make generalizations about habitat selection. Similarly, mean sage-grouse habitat use differed from random (when random is use in proportion to availability) for summer, winter, and nest relocation groups at the study area scale, which supports the hypothesis that sage-grouse select habitats with desirable characteristics for them.

For sage-grouse, not all sagebrush community types in the study area are equal (fig. 3, next page). Big sagebrush and mixed big sagebrush–bitterbrush habitats were preferred by all relocation groups. At all scales, big sagebrush–bitterbrush (mean across seasons and scales $S = 7.08$) had higher mean selection ratios than big sagebrush (mean $S = 2.63$, but not significant because of high variance, standard deviation = 9.04, and our conservative 95% confidence interval). Low-sagebrush dwarf shrublands were never used in the winter, so they had winter selection ratios of zero. Nine birds used sagebrush–shrubby cinquefoil but infrequently and generally only as a small proportion of a relocation's 200-meter (656 ft) buffer.

Sage-grouse avoid habitat differently during different seasons. For example, the only habitats that were significantly avoided at any scale in the winter were low-sagebrush ($S = 0$), big sagebrush–shrubby cinquefoil ($S = 0.46$), conifer forest ($S = 0.32$), aspen woodland ($S = 0.86$), and the unused habitats ($S = 0$). In addition, cottonwood riparian was the only non-sagebrush habitat class


(a) Grand Teton National Park
Selection Index
0
2
4
6
8
10
12
14
Low Sage
Big Sage–Bitterbrush
Sage-Cinquefoil
Big Sage
Disturbed
Riparian
Forb
Aspen
Low Hillside Vegetation
Grassland
Deciduous Shrub
Cottonwood


(b) Minimum Convex Polygon
Selection Index
0
2
4
6
8
10
12
14
Low Sage
Big Sage–Bitterbrush
Sage-Cinquefoil
Big Sage
Disturbed
Riparian
Forb
Aspen
Low Hillside Vegetation
Grassland
Deciduous Shrub
Cottonwood

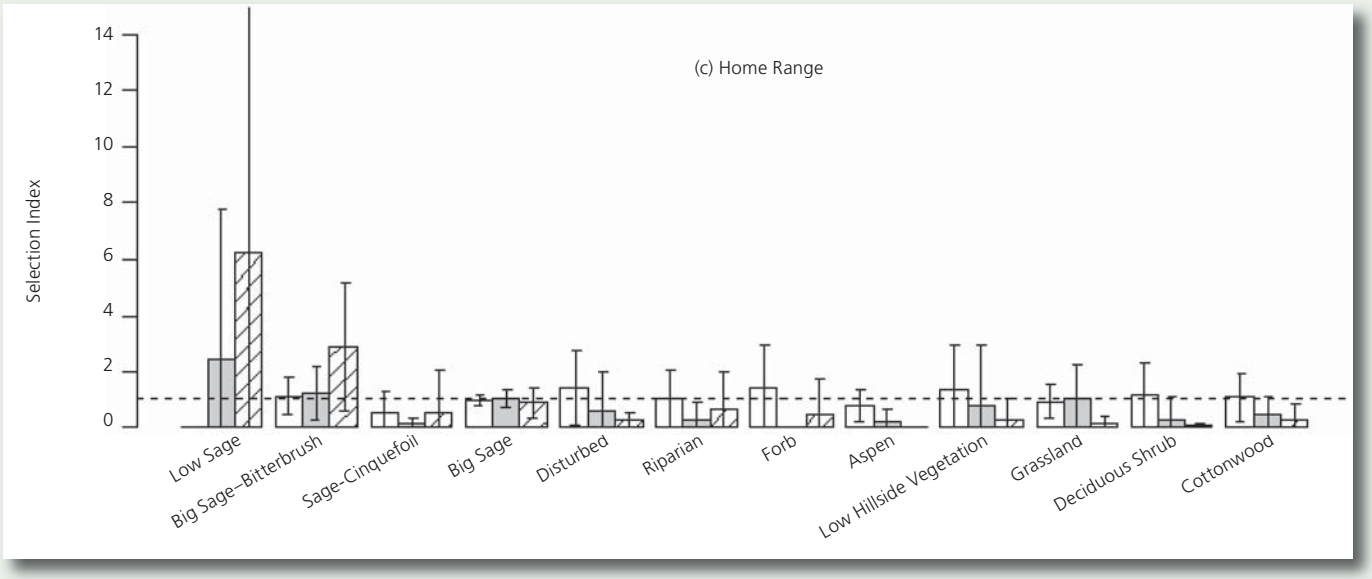

(c) Home Range
Selection Index
0
2
4
6
8
10
12
14
Low Sage
Big Sage–Bitterbrush
Sage-Cinquefoil
Big Sage
Disturbed
Riparian
Forb
Aspen
Low Hillside Vegetation
Grassland
Deciduous Shrub
Cottonwood

Figure 3 (left). Mean sage-grouse selection indices (observed/expected) for 12 habitat types at (a) study area (Grand Teton and surrounding areas), (b) minimum convex polygon, and (c) home-range scales in Grand Teton National Park, 1999–2003. White bars represent winter selection, shaded bars represent summer selection, and hatched bars represent nest site selection. Error bars show 95% confidence intervals. The dotted line at selection index = 1 represents the point at which observed use is in proportion to availability. The nesting habitat selection at the GRTE scale for big sage–bitterbrush continues beyond the figure to a selection index of 26.1. The upper limit of the 95% CI for summer big sage–bitterbrush at the GRTE scale extends beyond the figure to a selection index of 25.2.

Surprisingly, our population wintered in hills with a wide range of shrubby habitats and near trees, rather than in the homogenous sagebrush winter habitat reported in the literature.

with a significant positive selection ratio (S = 4.73), and this occurred in the winter season.

In summer, sage-grouse used only 4 of the 14 habitat classes proportionally to their availability. We used eigenanalysis (Calenge and Dufour 2006) to statistically describe habitat selection based on individuals' locations. The summer eigenanalysis, for example, explained 95% of the variation in habitat selection with only two habitat classes: big sagebrush and big sagebrush–bitterbrush. Because more habitats were used in the winter, the winter eigenanalysis at the same scale accounted for only 55% of the variation and yielded, in addition to big sagebrush and big sagebrush–bitterbrush, three other influential habitat classes: tall deciduous shrubland, exposed hillside, and human disturbed, all of which, though insignificant, had selection ratios greater than 1.

Nesting habitat was more uniform than winter or summer habitat (fig. 3). Mixed big sagebrush–bitterbrush (S = 26.07) and big sagebrush (S = 4.76) dominated nesting habitat, whereas other vegetation classes were only minimally present in the 200-meter (656 ft) buffers. Avoidance of non-sagebrush habitats typified nesting habitat selection (S = 0.21).

The minimum convex polygon (MCP) encompasses the entire landscape used by the population, and we built it using all 221 relocations. The MCP covered 47,278 hectares (116,824 ac) primarily in the valley floor but also up into the hills to the east and south of the main valley (fig. 2, page 45). Year-round home range (combined summer, winter, and nesting home range) spanned 9,414 hectares (23,262 ac). Winter home range (6,321 hectares [15,619 ac]) overlapped only 28% of the summer home range (4,366 hectares [10,788 ac]), indicating a difference between the seasonal habitats (fig. 2). Summer home range predominantly occupied the sagebrush flats in the center of the valley, whereas winter-use core areas were partially spread outward onto the hills that surround the valley floor. Slope measurements made in Grand Teton National Park vegetation plots were, on average, 96% steeper in sage-grouse winter home range than in summer home range (10% and 5%; Wilcoxon rank-sum test, $P < 0.01$).

Discussion

The pictures of sage-grouse habitat use provided by this study are an important starting point for research that connects habitat selection with fitness and population dynamics (e.g., Aldridge and Boyce 2007). In summer, the study area population avoided nearly all non-sagebrush habitats, which indicates that during our study period they did not need to seek resources in more moist or riparian areas. Surprisingly, our population wintered in hills with a wide range of shrubby habitats and near trees, rather than in the homogenous sagebrush winter habitat reported in the literature (Crawford et al. 2004; Carpenter et al. 2010). These results support the hypothesis that traditional, suitable winter habitat may be limiting in the study area, and further suggest that sage-grouse prefer to remain in sagebrush-dominated habitats but will seek required resources where they exist.

During our study period the Jackson Hole sage-grouse population selected atypical habitats in winter probably in search of exposed sagebrush for food, topography for shelter, or both, and this population's need for these resources superseded the usual avoidance of trees, which can contain raptor predators (Beck 1977; Connelly et al. 2004; Doherty et al. 2008). The hilly vegetation mosaic selected by wintering grouse, although not dominated by sagebrush, likely contained the only exposed patches of sagebrush. Wintering sage-grouse have been found to select for low sagebrush because of its high palatability (Connelly et al. 2004; Rosentreter 2005), but in the study area low sagebrush is likely snow-covered and unavailable during the winter.

Regardless of which resource birds were seeking when selecting nontraditional habitats, it does not reduce the fact that sage-grouse survived winters in a mosaic of vegetation types, includ-

ing cottonwood riparian forest, mixed tall deciduous shrubland, exposed hillside sparse vegetation, aspen forest and mixed grassland, as well as big sagebrush and bitterbrush shrublands. This suggests that sage-grouse may be able to use a wider range of habitats than previously thought (Connelly et al. 2004), but also demonstrates how dependent the species is on sagebrush and suggests that ideal sagebrush winter habitat may be limited in the study area.

Whether studying sage-grouse or other species with potential seasonally limited habitat, this research reminds us to include a large landscape scale such as the minimum convex polygon and to avoid preconceptions of habitat use.

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