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Original Article

Seasonal Movements of Greater Sage-grouse Populations in Utah: Implications for Species Conservation

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ABSTRACT Greater sage-grouse (*Centrocercus urophasianus;* sage-grouse) is considered an umbrella species for sagebrush (*Artemisia* spp.) landscapes in western North America. In 2015, the U.S. Fish and Wildlife Service determined sage-grouse unwarranted for protection under the Endangered Species Act (1973) because of conservation actions in priority areas. Understanding seasonal movements is key to delineation and assessment of priority conservation areas. We monitored radiomarked sage-grouse from 1998 to 2013 throughout Utah, USA, to determine seasonal movements. Maximum distances from nearest lek to nesting, summer, and winter locations across all radiomarked grouse averaged 2.20 km (90th percentile = 5.06 km), 3.93 km (90th percentile = 8.45 km), and 3.76 km (90th percentile = 7.15 km), respectively. Maximum movements from nest to summer, nest to winter, and between summer and winter locations across all radiomarked grouse averaged 5.77 km (90th percentile = 13.60 km), 11.77 km (90th percentile = 26.36 km), and 14.75 km (90th percentile = 30.77 km), respectively. Maximum distance from lek of capture to summer locations was greater for males than females, whereas females moved farther than males from lek to winter and summer to winter locations. Adult females moved farther than yearlings from lek to nest and summer to winter areas. The state of Utah's Sage-Grouse Management Areas included approximately 85% of the radiotelemetry seasonal locations and >95% when weighted by lek counts. Our results suggest that seasonal movements could be facilitated by increasing usable habitat space through management actions, as emphasized in Utah's sage-grouse plan. © 2016 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, conservation, greater sage-grouse, landscapes, priority conservation areas, Sage-Grouse Management Areas, seasonal movements, telemetry, Utah.

Greater sage-grouse (*Centrocercus urophasianus;* sage-grouse) require sufficient space and juxtaposition of different seasonal habitat types to meet their life-history requirements (Connelly et al. 2000, Knick and Connelly 2011). The sagebrush landscapes on which sage-grouse depend often transcend multiple jurisdictional boundaries, land ownerships, and land uses. Because sage-grouse are dependent on sagebrush (*Artemisia* spp.) landscapes in western North America (Schroeder et al. 1999), they are considered an umbrella or indicator species for other wildlife that inhabit these ecosystems (Knick and Hanser 2011).

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Sage-grouse populations have declined over recent decades because of habitat loss, degradation, and fragmentation and are estimated to currently occupy half of their original range (Schroeder et al. 2004, Garton et al. 2011). In 2010, the species was designated by the U.S. Fish and Wildlife Service (USFWS) as a candidate species for listing under the Endangered Species Act of 1973 (USFWS 2010). In 2015, the USFWS determined the species did not warrant Endangered Species Act protection because threats to the species were being mitigated by on-going range-wide conservation measures implemented in designated priority conservation areas (USFWS 2015). However, the USFWS is required by law to conduct a 5-year review of the species' status and population response to conservation actions to determine whether the species may warrant future Endangered Species Act protection.

Understanding seasonal movements for this at-risk species was key to identifying range-wide priority conservation areas (USFWS 2015). Sage-grouse seasonal habitats have generally been defined using 3 broad categories: breeding, summer, and winter (Connelly et al. 2000). Breeding habitats consist of areas where prelaying, lekking, nesting, and early brooding activities occur. Summer habitats primarily consist of late brooding areas. Winter habitat occurs in areas where sagebrush is available above the snow throughout the winter for food and cover (Connelly et al. 2000). Some populations may be considered nonmigratory, using a specific landscape to meet all their seasonal habitat requirements (Connelly et al. 2000). Other populations may migrate >50 km between seasonal habitats (Connelly et al. 2000, Leonard et al. 2000, Fedy et al. 2012). Within populations, individuals may exhibit varying movement strategies between seasonal habitats (Fedy et al. 2012, Reinhart et al. 2013).

Sage-grouse conservation planning within state and federal agencies has recently occurred using a strategic landscape management approach (Williams et al. 2004, Idaho Department of Fish and Game 2006, Doherty et al. 2011, Goble et al. 2012, Utah 2013). The USFWS Conservation Objectives Team report emphasized the need to focus management efforts on protecting and enhancing priority habitats as an essential mechanism for sage-grouse conservation (USFWS 2013). Priority conservation areas across sage-grouse range have been delineated for future conservation investment because they afford increased certainty that conservation actions will result in population persistence (Stiver et al. 2006, Doherty et al. 2011, USFWS 2013). A strategic approach to species conservation planning targets areas that are likely to yield the greatest returns to conservation investments (Margules and Pressey 2000, Schulte et al. 2008, Carvell et al. 2011). Doherty et al. (2011) and Fedy et al. (2012) stressed the need to include all seasonal habitat types, not just breeding habitats, within these priority areas. Fedy et al. (2012) demonstrated how priority conservation areas can be assessed using sage-grouse seasonal movements in Wyoming, USA, by using radio-marked individuals across multiple study areas, but called for more information from other studies to further validate this approach.

Current sage-grouse distribution and habitat in Utah, USA, tends to be fragmented and disjunct compared with other states (Beck et al. 2003, Schroeder et al. 2004). Historically, sage-grouse occurred in all of Utah's 29 counties (Beck et al. 2003). Current sage-grouse distribution in Utah is estimated to represent 40.9% (2.1% of which is Gunnison sage-grouse [*C. minimus*] range) of the historical distribution within the state in 26 counties (Beck et al. 2003). Currently, Utah's larger populations of sage-grouse inhabit sagebrush landscapes in west Box Elder, Rich, Wayne, Garfield, and Uintah counties. Smaller populations inhabit extant sagebrush habitats in southwest, central, and northeastern Utah (Beck et al. 2003). Although declines occurred in the 1960s, overall populations have been relatively stable since the mid-1980s (Beck et al. 2003, Garton et al. 2011).

The State of Utah published a state-wide plan (Plan; Utah 2013) to facilitate sage-grouse conservation and management actions. Utah's Plan was developed to protect habitat and associated populations of sage-grouse by designating priority areas for sage-grouse conservation actions (USFWS 2013). Utah's Plan delineated 11 Sage-Grouse Management Areas that stakeholders believed afforded the greatest conservation potential for populations and habitats (Fig. 1). The Utah Plan's approach was designed to encompass all seasonal habitats for each population (i.e., incorporate priority conservation areas). Because sage-grouse use large landscapes and strategic conservation is being implemented within priority conservation areas, there is a

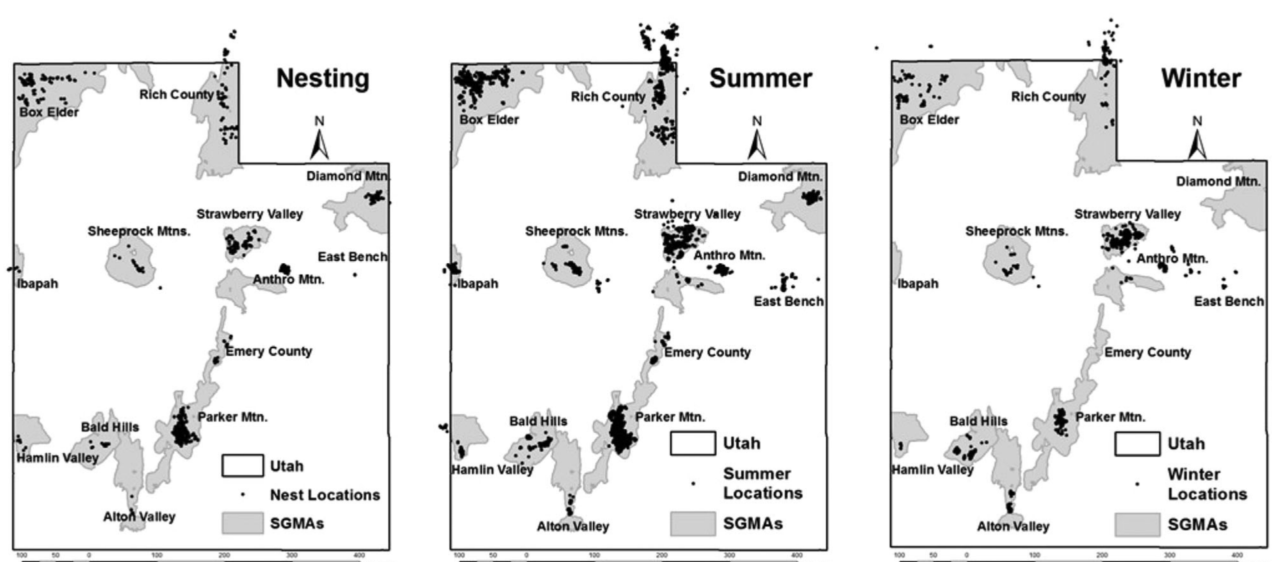

Figure 1. Maps of greater sage-grouse (*Centrocercus urophasianus*) study areas and radiomarked seasonal locations (black circles) during 1998–2013 in Utah, USA. Maps show nest, summer, and winter locations. Gray areas represent Utah's Sage-Grouse Management Areas.

need to understand seasonal movements and assess how well priority conservation areas in Utah incorporate seasonal locations. We used sage-grouse radiotelemetry-location data collected over 2 decades to map breeding (nest and early brooding), summer (late brooding and nonreproductive individuals), and winter-use locations and then determine where and how seasonal movements might differ among and within age-classes, sexes, and distinct populations based on habitat availability. Specifically, we evaluated the distance from breeding grounds (i.e., leks) to seasonal locations and described inter-seasonal movements to define recommended buffers for conservation. We also assessed the relationship between movement distance and habitat space. Lastly, we determined what percent of Utah's sage-grouse seasonal locations were encompassed by Utah's Sage-Grouse Management Areas.

STUDY AREA

Sage-grouse location data were compiled from sage-grouse populations at 13 study areas in Utah from 1998 to 2013 (Fig. 1). These study areas represented the majority of sage-grouse populations in Utah. All but 2 study areas were associated with Sage-Grouse Management Areas (Fig. 1). Populations in northern Utah inhabited sagebrush-steppe, while populations in central and southern Utah primarily used sagebrush semidesert (West 1983). Both were shrub-dominated sagebrush systems differentiated by an increased herbaceous component in higher latitude sagebrush-steppe systems compared with lower latitude sagebrush semidesert. Generally, big sagebrush (*A. tridentata*) varieties dominated most landscapes within occupied habitats with Wyoming (*A. t. wyomingensis*), basin (*A. t. tridentata*), and mountain (*A. t. vaseyana*) big sagebrush at lower, mid, and high elevations, respectively. Shallow soils supported inclusions of low (*A. arbuscula*) and black (*A. nova*) sagebrush across the state. Silver sagebrush (*A. cana*) was present at high-elevation mesic areas and there was limited distribution of three-tip sagebrush (*A. tripartita*) in northern Utah. Although statewide landownership in Utah was predominantly federal, private lands in the state provided approximately 50% of the current habitat for sage-grouse populations (Beck et al. 2003).

Beck et al. (2003) mapped the current distribution of sage-grouse within Utah. Most of the sage-grouse populations in the state were relatively small and inhabited isolated and remote landscapes (Beck et al. 2003). The largest sage-grouse populations in the state were associated with larger, contiguous sagebrush landscapes. We compared our Figure 1 with Beck et al. (2003) to classify population status relative to landscape characteristics. To evaluate seasonal movements, we assigned either "large continuous" or "small isolated" population status to each study area. Our study areas included West Box Elder County (large), Rich County (large; some birds were captured in or moved into Idaho), Diamond Mountain (large; Uintah County), East Bench (small; Uintah County), Anthro Mountain (small; Duchesne County), Strawberry Valley (small; Wasatch County), Sheeprock Mountains (small; Tooele and Juab counties), Ibapah (small; Tooele and Juab counties; some birds were captured in or moved into Nevada), Wildcat Knoll and Horn Mountain referred to as Emery County (small; Emery and Sevier counties), Parker Mountain (large; Wayne, Piute, and Garfield counties), Bald Hills (small; Iron County), Hamlin Valley (small; Iron County), and Alton Valley (small; Kane County; Fig. 1). Study areas of Anthro Mountain and East Bench were not incorporated into Sage-Grouse Management Areas because of current and potential anthropogenic disturbance and a lower certainty of return on future conservation investment (Utah 2013). Utah shared sage-grouse populations with all adjacent states except Arizona and New Mexico.

METHODS

We captured individual sage-grouse nocturnally using spotlights and dip-nets in the early spring near lek sites, although we trapped a few individuals during late summer or early autumn (Giesen et al. 1982). We sexed (male or female) and aged (yearlings or second year—SY; or adults or after second year—ASY) birds based on wing characteristics (Beck et al. 1975). We attached necklace-style 19–21-g radios (Advanced Telemetry Systems, Inc., Isanti, MN, USA; Holohil Systems, Ltd., Carp, ON, Canada; American Wildlife Enterprises, Monticello, FL, USA); radios were equipped with a motion detection for mortality signal and 24–36 months of battery life. Institutional Animal Care and Use Committee permit numbers from Utah State University were 2322, 2411, 2419, 2560, 1451, 2189, 942, 942R, 1194, 1404, 1332, and from Brigham Young University were 100302, 110301, 050301, 080402.

Throughout all seasons, we used a handheld global position system (GPS) unit to record a position for radiomarked bird locations within a few meters of where we tracked birds to, flushed birds, or aerially located birds with fixed-wing aircraft (Universal Transverse Mercator [UTM] NAD83 Zone 12). Only one study, located in northern Rich County and southeastern Idaho (Fig. 1), used triangulation to obtain UTMs. To approximate locations by triangulation, we used LOCATE III version 3.18 (www.locateiii.com) with $\geq$3 bearings from different locations (UTMs), where the first 2 bearings were approximately 45° from each other and the third bearing bisected the intersection of the first 2 bearings. We categorized locations throughout Utah as nest, brood, or nonbreeding adult locations.

We located radiomarked females at their nest sites using telemetry and binoculars. We did not purposely flush females from their nests because of the propensity of sage-grouse females to abandon nests once disturbed (Connelly et al. 2011*b*). If $\geq$1 egg hatched, we considered the nest successful and followed brood females through early and late brooding activities. We took care not to flush chicks during brood monitoring, and we used female "broody" behavior (e.g., did not join groups of other adult grouse; held tight when observer was nearby; broken-wing display if flushed) as a surrogate for documenting extant chicks. We completed concerted efforts at the end of the brooding period (42 or 50 days) to document live chicks; and in Parker Mountain, Strawberry Valley, and West Box Elder, we used pointing dogs to locate chicks at the end of the brooding season (Dahlgren et al. 2010, 2012). We did not evaluate distance moved by brood fate because broods that survived longer had more opportunity to move farther. We located males and nonreproductive females sporadically throughout the summer and located all radiomarked birds irregularly during the autumn and winter. At least one flight with fixed-wing aircraft occurred during the autumn and winter in all areas and years studied.

The organizations from which data originated followed their quality assurance and quality control procedures before we received the databases. Once we compiled these data into a single database, we completed another quality assurance and quality control process to ensure data were consistent among study areas and projects. For example, we evaluated location accuracy, making note of suspect locations, and contacted original personnel who collected the data if such locations were identified. We censored from the statewide database any data points that could not be confirmed as accurate or corrected. We performed spatial analyses using ArcGIS 10.2 and R (R Core Team 2013) packages *sp* (Pebesma and Bivand 2005, Bivand et al. 2013) and *rgeos* (Bivand and Rundel 2013).

We determined inter-seasonal habitat movements using UTMs to calculate the Euclidean distance (m) between points. We censored any individuals captured outside of the spring lekking season (1 Mar–31 May) from nearest lek and lek of capture calculations. We used the Utah Division of Wildlife Resources (UDWR) statewide sage-grouse lek database to map lek locations (http://wildlife.utah.gov/uplandgame/sage-grouse/, Greater Sage-Grouse maps link). Because inaccuracies in lek location information existed in previous data sets, prior to conducting the analysis, all known lek locations were verified in 2013 by UDWR biologists. The nearest lek was defined as the lek with the minimal distance from a given radiomarked bird location with a UDWR lek count of >1 for ≥ 1 year in the previous 10 years (i.e., occupied) or a newly discovered lek that had been counted for <2 years (i.e., undetermined). The lek of capture was defined as the nearest lek (same requirements as above) to the original capture location of the radiomarked bird.

We defined nest locations as a confirmed visual (using binoculars) location of the radiomarked female on the nest. Because renesting rarely occurred in our study areas, we only considered first nesting attempts each year. Summer locations included all radiomarked sage-grouse locations from 15 June to 31 August. For some analyses, we separated out brood locations during the summer; where brood was defined as a radiomarked female with ≥ 1 chick(s) present. Because summer and winter locations could have >1 location/individual unit (i.e., a single brood, or individual bird), we used only the maximum distance for each individual-by-year. We used maximum distance because our objectives were to provide management recommendations that incorporated the spatial extent needed to support this landscape species (Knick and Connelly 2011). We defined winter locations as any radiomarked sage-grouse (male or female) location from 1 November to 1 March. For seasonal movements, we accounted for sex, age (second year—SY; or after second year—ASY), and nest fate (success vs. unsuccessful) to assess whether these factors influenced, or were influenced by, movement distances (see Data Analysis below).

From 2003 to 2010, radiomarked sage-grouse were translocated from other study areas within Utah and released in Strawberry Valley and Anthro Mountain (Baxter et al. 2008, Gruber 2012). Translocated sage-grouse, being new to their available habitat, have the potential to make movements different from those of resident birds (Baxter et al. 2013). To assess this potential, we determined nest and brood location distances from nearest lek and lek of capture for translocated versus resident birds in both Strawberry Valley and Anthro Mountain. For analysis, the lek of release was a substitute for lek of capture for translocated birds. We then compared these distances using a 95% confidence interval of the difference of means and, similar to Baxter et al. (2008), found no differences in movements between translocated and resident birds for the Strawberry Valley study area (Supporting Information Table S1). Therefore, we included translocated with resident radiomarked bird locations for the Strawberry Valley study area in our movement analyses. We found no difference for nest and brood distances to nearest lek for Anthro Mountain study area; however, translocated birds had farther nest and brood locations from the lek of release (i.e., surrogate for lek of capture) than resident birds. Therefore, we censored translocated birds for the Anthro Mountain study area from lek of capture analyses.

To determine what percent of sage-grouse telemetry-based locations were included in Sage-Grouse Management Areas, we overlaid Utah's Sage-Grouse Management Area spatial data (i.e., an ESRI ArcGIS 10.1.2 shapefile) on known seasonal (nest, brood, summer, and winter) location data. For study areas abutting state borders, we did not include locations outside of the state of Utah when determining the percentage of locations within Sage-Grouse Management Area boundaries. Because the number of locations varied by individual bird and study area, our data had the potential to bias the percentage of locations covered by Sage-Grouse Management Area boundaries toward study areas with more locations per individual. We calculated individual study area weights to alleviate this bias. Study area weights were generated by creating a convex hull around all seasonal locations for each study area. We then used counts of active leks within the study area convex hull for the years each study area was monitored to determine the mean number of males for each lek. We then summed mean males per lek for all leks within each study area convex hull. Each study area weight was then calculated by dividing the sum of males per lek for each study area by the total sum of males per lek across all study areas. The study area weight was then multiplied by percent of locations within the Sage-Grouse Management Area boundary for each study area, and then these products were summed across all study areas to represent the weighted proportion of nest, summer, and winter locations within Sage-Grouse Management Area.

Because sage-grouse populations across Utah inhabited sagebrush landscapes that varied in size (Beck et al. 2003, Schroeder et al. 2004), we evaluated the effect of usable space (i.e., habitat space) on seasonal movement patterns. Usable space can be defined as any point on a landscape where habitat is compatible with the adaptations (i.e., physical, behavioral, and physiological) of a species in a time-unlimited sense (adapted from Guthery 1997). We assessed the effects of usable space using nest to maximum brood-location distance. We buffered successful nests with the 90th percentile (Fedy et al. 2012) distance for maximum within-year brood movements for all study areas (12.84 km). We then used a vegetation data layer that consisted of 9 cover types (Colorado Plateau Mixed Low Sagebrush Shrubland, Wyoming Basins Dwarf Sagebrush Shrubland and Steppe, Great Basin Xeric Mixed Sagebrush Shrubland, Inter-Mountain Basin's Big Sagebrush Shrubland, Columbia Plateau Low Sagebrush Steppe, Inter-Mountain Basin's Big Sagebrush Steppe, Inter-Mountain Basins Montane Sagebrush Steppe, Inter-Mountain Basin's Semi-Desert Shrub-Steppe, Shrubland Alliance) from the inter-agency Landscape Fire and Resource Management Planning Tools Project (LANDFIRE; http://www.landfire.gov; Rollins 2009) representing areas dominated by sagebrush (which we assumed to be potential sage-grouse habitat) to calculate the proportion of habitat space (i.e., usable space) within the 12.84-km nest buffer. Because disturbances to habitat (e.g., fire) may have occurred over the study period, we used LANDFIRE vegetation data layers from 2001, 2008, 2010, and 2012 to match vegetation conditions to brood location dates as best we could. Additionally, we used annual LANDFIRE disturbance layers to classify areas labeled as "medium" or "high" severity disturbance as nonhabitat. The brood movement distances were then regressed on the proportion of habitat space within the buffer to evaluate our hypothesis that greater proportions of habitat space would correlate positively with farther movement distances (see Data Analysis below). Additionally, if habitat space affected movements we expected an increase in variability of movement distances with increasing space; in other words, the option for larger movements was more available.

Data Analysis

We calculated mean, standard error, median, minimum, maximum, and the 5th, 90th, and 95th percentiles for each seasonal movement (including distance to nearest lek and lek of capture) by small, large, and all populations. Summary statistics for each seasonal movement by study area can be found in Supporting Information (Tables S1–14). We used a 95% confidence interval of the difference of means to test for differences in female age, sex class, and nest fate for seasonal movement distances (see Table 1 for a list of seasonal movement comparisons).

To evaluate whether brood movements were related to habitat space for each study area, we used a weighted least-squares linear regression of maximum distance broods moved on proportion of habitat space within the 12.84-km nest buffer, where age of the brood (i.e., days survived) was the weighted value (R Core Team 2013; http://stat.ethz.ch/R-manual/R-patched/library/stats/html/lm.html). We weighted by brood age because broods that survived longer had more opportunity to move farther from their nests; thus, distances associated with these broods provided more certainty than those associated with younger broods. Maximum distance a brood moved was log transformed to meet assumptions of normality for a least-squares linear regression. We used $\alpha = 0.05$ to test for statistical significance in our regression analysis.

RESULTS

We used data for seasonal locations from 1,242 female and 454 male radiomarked sage-grouse to conduct our study. On average, adult females located their nests 0.29 km farther away from the nearest lek and 1.11 km from lek of capture compared with yearling females (Table 2). Successful nests were located 0.31 km, on average, farther from the nearest lek than their unsuccessful counterparts (Table 3). In addition, adult females moved an average of 3.07 km farther between their maximum summer and winter locations compared with yearling females (Table 2). We found no differences in movements by age class for males (Table 4). On average, males moved 1.38 km farther than females from lek of capture in the summer, but females moved 0.68 km farther than males from the nearest lek during the winter (Table 5). In addition, females moved an average of 3.5 km farther

Table 1. Comparisons made for seasonal movement distances and age class, sex, and nest survival fate for greater sage-grouse (*Centrocercus urophasianus*) populations during 1998–2013 in Utah, USA. N/A is not applicable. The Table column represents the numbered tables within the text below.

Seasonal movement distance comparison	Age, sex, or fate comparison	Table
Nest to nearest lek	Female age and nest fate	2, 3, 6
Nest to lek of capture	Female age and nest fate	2, 3
Nest to max. brood location	N/A	6
Nest to max. summer location	Female age	2, 6
Nest to max. winter location	Female age	2, 6
Nearest lek to max. brood location	Female age	2
Nearest lek to max. summer location	Sex and male age	4, 5, 7
Nearest lek to max. winter location	Sex and male age	4, 5, 7
Lek of capture to max. brood location	Female age	2
Lek of capture to ma. summer location	Sex and male age	4, 5
Lek of capture to max. winter location	Sex and male age	4, 5
Max. summer to winter locations	Sex and age	2, 4, 5, 7

Table 2. Female greater sage-grouse (*Centrocercus urophasianus*) age-class comparisons for seasonal movements for combined samples across all study areas, during 1998–2013 in Utah, USA. SE, standard error; LCL, lower confidence limit for the 95% confidence intervals of the difference in means; UCL, upper confidence limit for the 95% confidence intervals of the difference in means.

Movement comparison[a]	Female age[b]	*n*	$\bar{x}$ (km)	SE	LCL	UCL
Nest to nearest lek	SY	228	1.97	0.12	0.02	0.56
	ASY	659	2.26	0.08		
Nest to lek of capture	SY	175	5.04	0.39	0.17	2.06
	ASY	552	6.15	0.29		
Nearest lek to max. brood location	SY	101	3.85	0.28	−0.47	0.8
	ASY	282	4.02	0.16		
Lek of capture to max. brood location	SY	72	8.02	0.88	−1.53	2.44
	ASY	207	8.47	0.49		
Nest to max. summer location	SY	157	5.95	0.50	−1.65	0.74
	ASY	392	5.50	0.35		
Nest to max. winter location	SY	29	10.69	1.44	−2.19	5.07
	ASY	85	12.13	1.14		
Max. summer to winter locations	SY	80	13.92	1.10	0.25	5.88
	ASY	184	16.99	0.91		

[a] Summer movements include brood and nonbreeding female locations 15 Jun–31 Aug. Winter movements include female locations 1 Nov–1 Mar. Brood locations include brood female locations 15 Jun–31 Aug.
[b] SY, second year; ASY, after second year.

between their maximum summer and winter locations compared with males (Table 5). Regardless of whether sage-grouse were in small isolated populations or large continuous ones, females placed their nests an average of 2.20 km (min. = 0.04 km, max. = 11.91 km, 90th percentile = 5.06 km) from the nearest lek (Table 6).

Table 3. Female greater sage-grouse (*Centrocercus urophasianus*) nest-fate comparisons for seasonal movements for combined samples across all study areas during 1998–2013 in Utah, USA. SE, standard error; LCL, lower confidence limit for the 95% confidence intervals of the difference in means; UCL, upper confidence limit for the 95% confidence intervals of the difference in means.

Movement comparison	Nest fate[a]	*n*	$\bar{x}$ (km)	SE	LCL	UCL
Nest to nearest lek	U	379	2.05	0.09	0.05	0.56
	S	496	2.36	0.09		
Nest to lek of capture	U	315	6.43	0.41	−1.63	0.35
	S	397	5.80	0.30		

[a] S, successful; U, unsuccessful.

Whether in small or large populations females moved on average 11.77 km (min. = 0.63 km, max. = 40.33 km, 90th percentile = 26.36 km) from nest to winter locations (Table 6). Regardless of sex class, grouse moved an average of 14.75 km (min. = 0.24 km, max. = 58.31 km, 90th percentile = 30.77 km) from summer to winter locations (Table 7). Irrespective of being in small isolated or large continuous populations, grouse moved on averaged 3.93 km (min. = 0.07 km, max. = 24.54 km, 90th percentile = 8.45 km) from nearest lek to maximum summer locations (Table 7). However, grouse in small isolated habitats moved farther ($\bar{x}$ = 4.14 km, SE = 0.16, min. = 0.17 km, max. = 18.15 km, 90th percentile = 8.65 km) than grouse in large contiguous habitats ($\bar{x}$ = 2.79 km, SE = 0.17, min. = 0.16 km, max. = 25.78 km, 90th percentile = 4.98 km) from nearest lek to maximum winter locations (Table 7).

Overall, we found that 88%, 78%, and 89% of nest, summer, and winter locations, respectively, were within Sage-Grouse Management Areas. After weighting by male lek counts, 96%, 95%, and 95% of nest, summer, and winter

Table 4. Male greater sage-grouse (*Centrocercus urophasianus*) age-class comparisons for seasonal movements for combined samples across all study areas during 1998–2013 in Utah, USA. SE, standard error; LCL, lower confidence limit for the 95% confidence intervals of the difference in means; UCL, upper confidence limit for the 95% confidence intervals of the difference in means.

Movement comparison[a]	Male age[b]	*n*	$\bar{x}$ (km)	SE	LCL	UCL
Nearest lek to max. summer location	SY	28	4.87	0.80	−0.42	2.82
	ASY	253	3.67	0.19		
Lek of capture to max. summer location	SY	28	9.38	1.23	−4.65	0.76
	ASY	253	11.33	0.60		
Nearest lek to max. winter location	SY	14	3.43	0.62	−1.11	1.54
	ASY	133	3.22	0.25		
Lek of capture to max. winter location	SY	14	9.35	1.93	−4.29	4.05
	ASY	133	9.47	0.86		
Max. summer to winter locations	SY	6	12.54	3.25	−6.86	6.82
	ASY	78	12.56	1.13		

[a] Summer movements include male locations 15 Jun–31 Aug. Winter movements include male locations 1 Nov–1 Mar.
[b] ASY, after second year; SY, second year.

Table 5. Greater sage-grouse (*Centrocercus urophasianus*) sex-class comparisons for seasonal movements for combined samples across all study areas during 1998–2013 in Utah, USA. SE, standard error; LCL, lower confidence limit for the 95% confidence intervals of the difference in means; UCL, upper confidence limit for the 95% confidence intervals of the difference in means.

Movement comparison[a]	Sex	n	$\bar{x}$ (km)	SE	LCL	UCL
Nearest lek to max. summer location	F	1,014	3.94	0.11	−0.44	0.44
	M	290	3.94	0.20		
Lek of capture to max. summer location	F	919	9.71	0.29	0.16	2.59
	M	287	11.09	0.55		
Nearest lek to max. winter location	F	364	4.04	0.18	−1.29	−0.07
	M	154	3.36	0.25		
Lek of capture to max. winter location	F	363	14.26	0.58	−6.71	−2.88
	M	152	9.47	0.78		
Max. summer to winter locations	F	267	16.08	0.72	−5.99	−1.01
	M	86	12.58	1.04		

[a] Summer movements include brood and nonbreeding female and male locations 15 Jun–31 Aug. Winter movements include female and male locations 1 Nov–1 Mar.

locations, respectively, fell within Sage-Grouse Management Areas.

Females moved farther ($\bar{x} = 6.95$ km, SE = 0.46, min. = 0.00 km, max. = 57.45 km, 90th percentile = 15.72 km) in large populations compared to small populations ($\bar{x} = 4.47$ km, SE = 0.33, min. = 0.02 km, max. = 346.40 km, 90th percentile = 9.96 km) from nest to summer locations. Specifically, broods in larger contiguous landscapes of sagebrush habitat moved greater than twice as far ($\bar{x} = 6.99$ km, SE = 0.50, $n = 226$) from their nests compared with broods in small more isolated habitats ($\bar{x} = 3.25$ km, SE = 0.29, $n = 156$; Table 6; Fig. 2). For every one-unit (i.e., percent) increase in habitat space within the 12.84-km buffer there was a 1.7% increase in the maximum distance a brood moved from the nest (slope = 0.017, $P \leq 0.0001$; $r^2 = 0.13$; Fig. 2).

DISCUSSION

Contemporary conservation planning for sage-grouse provides a species-specific example of the need for increased knowledge of seasonal movements for strategic landscape-management approaches (Goble et al. 2012, USFWS 2015). Although individual sage-grouse in Utah moved considerable distances, the seasonal movements we reported for Utah's sage-grouse populations were generally less than those reported range-wide. The differences we observed may reflect the localized and naturally noncontiguous nature of many sagebrush habitats in the southern Great Basin and Colorado Plateau (Beck et al. 2003, Schroeder et al. 2004,

Table 6. Distances (km) of female greater sage-grouse (*Centrocercus urophasianus*) movements by study area size during 1998–2013 in Utah, USA. SE, standard error; LCL, lower confidence limit for the 95% confidence intervals of the difference in means; UCL, upper confidence limit for the 95% confidence intervals of the difference in means; Min. and Max. are the minimum and maximum distances for individual grouse. The 90th percentile of distances is represented by column p90.

Movement comparison[a]	Study area	n	$\bar{x}$ (km)	SE	LCL	UCL	Min.	Max.	p90
Nest to nearest lek	Large	531	2.20	0.08	−0.25	0.25	0.04	9.76	5.08
	Small	396	2.20	0.10			0.10	11.91	4.87
	Total	927	2.20	0.06			0.04	11.91	5.06
Nest to max. summer location	Large	295	6.95	0.46	−3.95	−1.37	0.00	57.45	15.72
	Small	270	4.47	0.33			0.02	36.40	9.96
	Total	565	5.77	0.29			0.00	57.45	13.60
Nest to max. winter location	Large	17	11.90	2.72	−5.90	5.57	0.74	37.81	26.61
	Small	97	11.74	0.98			0.63	40.33	25.85
	Total	114	11.77	0.92			0.63	40.33	26.36
Nest to max. brood location	Large	226	6.99	0.50	−4.88	−2.59	0.12	42.57	15.71
	Small	156	3.25	0.29			0.02	24.23	7.87
	Total	382	5.46	0.33			0.02	42.57	12.84

[a] Summer movements include brood and nonbreeding female locations 15 Jun–31 Aug. Winter movements include female locations 1 Nov–1 Mar. Brood locations include brood female locations 15 Jun–31 Aug.

Table 7. Distances (km) of greater sage-grouse (*Centrocercus urophasianus*) movements by study area size during 1998–2013 in Utah, USA. SE, standard error; LCL, lower confidence limit for the 95% confidence intervals of the difference in means; UCL, upper confidence limit for the 95% confidence intervals of the difference in means. Min. and Max. are the minimum and maximum distances for individual grouse. The 90th percentile of distances is represented by column p90.

Movement comparison[a]	Study area	n	$\bar{x}$ (km)	SE	LCL	UCL	Min.	Max.	p90
Nearest lek to max. summer location	Large	543	3.88	0.12	−0.27	0.44	0.07	21.14	7.75
	Small	749	3.96	0.13			0.11	24.54	9.20
	Total	1,292	3.93	0.09			0.07	24.54	8.45
Nearest lek to max. winter location	Large	178	2.79	0.17	0.88	1.82	0.16	25.78	4.98
	Small	447	4.14	0.16			0.17	18.15	8.65
	Total	625	3.76	0.13			0.16	25.78	7.15
Max. summer to winter locations	Large	72	16.57	1.49	−5.40	0.92	0.85	50.05	38.09
	Small	309	14.32	0.62			0.24	58.31	29.77
	Total	381	14.75	0.58			0.24	58.31	30.77

[a] Summer movements include brood and nonbreeding female and male locations 15 Jun–31 Aug. Winter movements include female and male locations 1 Nov–1 Mar.

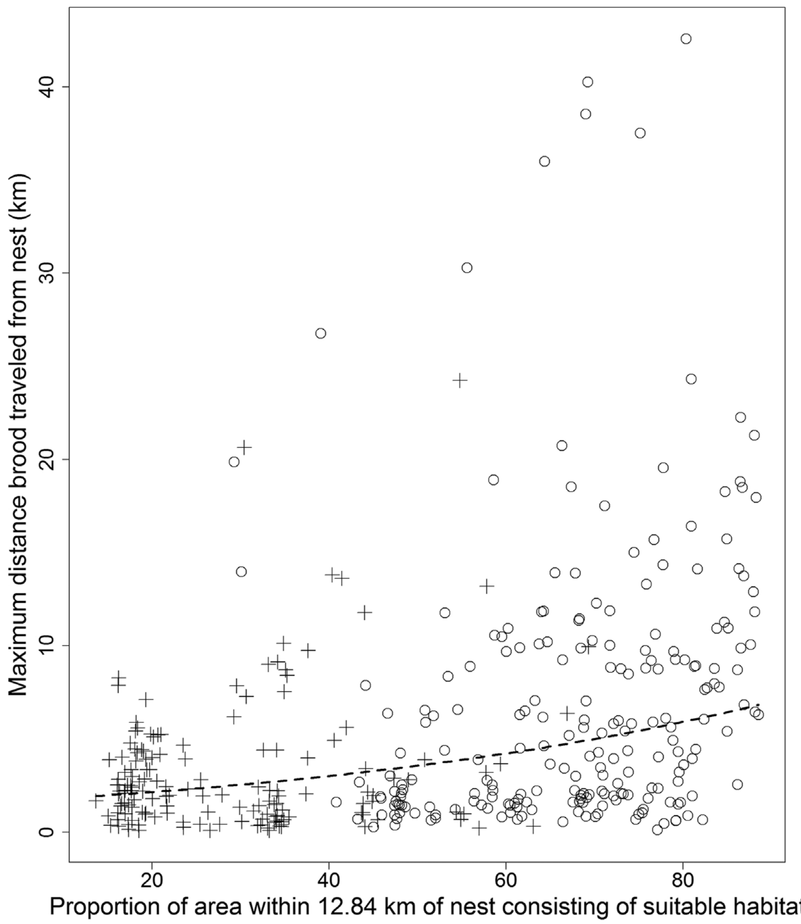

Figure 2. Maximum greater sage-grouse (*Centrocercus urophasianus*) brood movements from their nest site location plotted against the proportion of the area that is potential sagebrush (*Artemisia* spp.) habitat in Utah, USA, during 1998–2013. Circles symbolize the large contiguous study areas and crosses symbolize the small isolated study areas. The dotted line is the predicted movements from the weighted least-squares linear regression.

UDWR 2009, Fedy et al. 2012). For example, Fedy et al. (2012) reported farther average and maximum seasonal movement distances for sage-grouse in Wyoming where there was larger and more contiguous sagebrush habitats than in Utah (Schroeder et al. 2004). We also documented considerable variation by individuals within study areas, as demonstrated by our minimum and maximum values for specific seasonal movements.

To our knowledge, no other published studies have assessed sage-grouse movements based on differences in habitat space availability for each population. We found that radiomarked sage-grouse females and their broods in larger more contiguous populations moved farther than broods in smaller more isolated populations. The sage-grouse populations located within Alton Valley, Ibapah, Sheeprock Mountains, Bald Hills, Hamlin Valley, Anthro Mountain, East Bench, Strawberry Valley, and Emery County study areas inhabited relatively small, spatially isolated seasonal habitats surrounded by a generally unsuitable and fragmented landscape (Beck et al. 2003, UDWR 2009). Conversely, the larger sage-grouse populations that inhabited Parker Mountain, Rich County, West Box Elder, and Diamond Mountain study areas had access to larger, contiguous sagebrush landscapes; females with broods moved farther in correlation with the available space in these areas. Fedy et al. (2012) suggested similar habitat factors (e.g., fragmentation, availability) influenced nest to summer movements in Wyoming. We speculate the difference we observed between Utah's small and large populations during brooding activities reflected the increased availability and connectivity of seasonal habitats (i.e., usable space) afforded by larger scale contiguous sagebrush landscapes. However, our nest to brood or summer distances, even in our larger populations, were generally less than those reported in other studies (Klebenow and Gray 1968, Connelly et al. 1988, Fedy et al. 2012).

Conversely, small populations moved greater distances than large populations from nearest lek to winter locations. Hagen et al. (2001) suggested grouse populations in more fragmented landscapes required larger extents to meet their resource needs. Similar to Schroeder and Robb (2003), we suggest the longer movements to winter areas in small populations were an adaptation to isolated and fragmented habitat in these areas (Beck et al. 2003). For example, Sheeprock Mountains, Bald Hills, Strawberry Valley, and Anthro Mountain populations moved considerable distances from more isolated high-elevation breeding habitats to lower elevation wintering areas. Grouse in large populations such as West Box Elder and Parker Mountain generally moved down in elevation, but moved shorter distances with more contiguous breeding and winter habitat (Fig. 1).

The differences we found in seasonal movements between large and small populations suggest sage-grouse populations in Utah may benefit from conservation actions implemented to increase usable space (e.g., treatment of conifers encroaching into sagebrush communities) in 2 notable ways. First, because brood movements were confined to the available habitat space, increased habitat space adjacent to current breeding habitat could readily be used by sage-grouse. For example, sage-grouse in Utah have been shown to occupy areas of sagebrush encroached by conifers post-tree removal (Cook 2015, Sandford et al. 2015). This response has been immediate in areas that exhibited limited habitat space (Frey et al. 2013). Moreover, recent research has shown increased sage-grouse brood survival in association with conifer removal areas (C. Sandford, Utah State University, unpublished data). Brood survival, and more specifically survival of individual chicks, has been shown to influence sage-grouse population growth rates (Taylor et al. 2012, Dahlgren et al. 2016). Second, for small populations, increasing habitat space near breeding habitats may decrease fragmentation and reduce the distance they currently move through unsuitable habitats to wintering areas. Beck et al. (2006) found juvenile sage-grouse that moved farther distances to wintering areas experienced lower survival rates. Adult survival is the most important factor influencing rates of sage-grouse population growth (Taylor et al. 2012, Dahlgren et al. 2016). Although more research is needed to better understand the mechanisms influencing sage-grouse response to increases in habitat space, our observations of sage-grouse seasonal movements and other studies cited herein suggest the potential for a positive effect.

Fidelity to areas used in previous seasons may also influence movements of sage-grouse if they by-pass available habitats for more familiar areas (Wallestad 1971, Berry and Eng 1985, Schroeder et al. 1999, Connelly et al. 2000). Specifically, nest-area fidelity, where a female selects a specific area (less than a few hundred meters) in consecutive years for nest sites rather than randomly selecting from the available landscape, could influence adult female movements during the breeding period (Fischer et al. 1993, Peck et al. 2012). We did not assess fidelity to seasonal habitats by individuals.

Aldridge (2001) reported that seasonal variation in precipitation may also affect female sage-grouse and brood movements. He reported that radiomarked females and their broods moved less in wet than dry years (Aldridge 2001). Because our study period encompassed several years, which included variability in precipitation patterns, our data captured this variation in seasonal movements.

Our average (2.20 km) and 90th percentile (5.06 km) radiomarked female movements from nearest lek to nest were similar to distances reported by Coates et al. (2013). We found no difference in nearest lek to nest distances for small isolated and large contiguous habitats and associated populations. Because of the uniformity of nest to nearest lek distance in the populations studied, regardless of the available habitat space, and given the fact that these distances were consistent with other studies (Coates et al. 2013), we suggest these distances may reflect general sage-grouse breeding-habitat space requirements (Connelly et al. 2011*a*). As such, management decisions implemented under the Utah Plan (Utah 2013) and others should incorporate these distances when prioritizing actions to conservation of sage-grouse nesting habitat.

Successful nests were located farther from the nearest lek than unsuccessful nests. Differences in nest survival based on distance from the nearest lek may have been an artifact of the number of adult females in the sample population. Adult females tend to move farther from leks and have greater nest survival than juveniles (Dahlgren et al. 2016). However, because the mean distances from nearest lek for successful and unsuccessful nests were within a few hundred meters, this observation may not have important management implications.

Overall, the summer to winter movements for the sage-grouse populations we studied were similar to those reported in other studies (mean = 10–18 km) for various age classes (Connelly et al. 1988, Beck et al. 2006, Bruce et al. 2011, Fedy et al. 2012). However, monitoring during the winter was limited to a few annual fixed-wing aircraft flights per study area and ground searches were usually precluded by snow levels for relocating sage-grouse marked with very high frequency radiocollars during the winter. The increased deployment of GPS transmitters on sage-grouse to determine winter habitat use will likely provide better information to develop management actions to conserve winter habitats (Utah Wildlife In Need Foundation 2011).

Conservation buffers are an important consideration for sage-grouse management (Manier et al. 2014, USFWS 2015). Coates et al. (2013) argued leks are a reasonable focal point for sage-grouse management and best management practices for sage-grouse are often focused on leks and a buffered zone to protect populations and habitat. Some agencies have used distances of $\leq$1 km from leks to protect sage-grouse habitat (Connelly et al. 2000). However, our seasonal movement data, and that in other studies, suggest management buffers that only incorporate breeding (lek, nest, and early brooding) habitats may fail to protect key summer and wintering habitats (Doherty et al. 2011, Fedy et al. 2012). Fedy et al. (2012) emphasized the need to account for all seasonal habitats for sage-grouse conservation and reported that 85% of summer and 65% of winter locations were within Wyoming's core 75 areas, although percentages were greater in core 100 areas. Wyoming's core 75 and core 100 areas are the smallest buffer sizes around leks necessary to contain 75% and 100% of sage-grouse breeding populations, respectively (Doherty et al. 2011).

Conservation buffers have also often been utilized to mitigate the potential effects of energy developments and their related infrastructure on sage-grouse habitat. Indirect disturbance to sage-grouse from energy development can occur as far as 19 km from infrastructure (Naugle et al. 2011). Johnson et al. (2011) reported that lek count trends can be negatively related to the number of communication towers within 18 km of leks. Messmer et al. (2013) found that anthropogenic disturbances often consisted of multiple features (e.g., powerlines with nearby roads) potentially confounding the influence assessed for specific feature types (e.g., powerlines, wells, etc.). In Wyoming, wintering grouse were negatively affected by increasing well densities within a 2×2-km area (Doherty et al. 2008). LeBeau et al. (2014) found increased rates of sage-grouse nest and brood survival with increasing distance from wind-energy turbines. To mitigate these negative impacts, many federal and state management plans have adopted a 1-km buffer for tall structures (Messmer et al. 2013). Connelly et al. (2000) suggested a 3-km buffer within all seasonal habitats for construction of tall structures. Our data suggest the actual size of conservation buffers required to conserve breeding habitats in Utah will vary based on the amount of habitat space used by the population. To conserve breeding and summer habitats in Utah we suggest buffer distances of 5 km and 8 km, respectively. To be effective, however, conservation buffers should include all seasonal habitats, and we suggest that our 90th percentile values describe the potential landscape available to our populations (Fedy et al. 2012).

Some of the sage-grouse radiomarked in the Hamlin Valley, Ibapah, and West Box Elder used seasonal habitats in Nevada. Similarly, several sage-grouse radiomarked in West Box Elder, Rich County, and Diamond Mountain used seasonal habitats in Idaho, Wyoming, and Colorado. Reinhart et al. (2013) recorded inter-seasonal movements by sage-grouse across multiple state boundaries in the West Box Elder study area. Because of our recorded seasonal movements and the associated sagebrush landscapes, we suggest West Box Elder, Rich County, and Diamond Mountain provided adequate seasonal habitats and available space to improve the likelihood of persistence in Utah, while Ibapah and Hamlin Valley populations likely depend on habitats within Nevada. We reemphasize the critical need for a strategy to work with partners across political boundaries (Reinhart et al. 2013).

Utah's Sage-Grouse Management Areas, delineated by the state's sage-grouse conservation plan, included approximately 85% of the radiotelemetry seasonal locations and >95% when weighted by lek counts. However, the seasonal movement distances we measured from leks would not have accounted for undiscovered leks on the landscape. In nearly every study area, previously undiscovered leks were detected after research activities began. Therefore, lek searches should be conducted in areas of conservation concern to ensure adequate protection of important habitats.

MANAGEMENT IMPLICATIONS

Our results offer a framework to provide more certainty to sage-grouse management decision-making in Utah and other areas with isolated or fragmented habitats. For example, the conservation buffers we recommend can provide more certainty for protecting habitats important to current sage-grouse populations in Utah. Our reported seasonal movements indicate augmented usable habitat space could be readily occupied by sage-grouse with potential benefits to population growth. Concomitantly, the Utah state Plan has placed an emphasis on increasing the useable habitat space for Utah's sage-grouse populations. However, we caution that because sagebrush systems respond over long time frames to restoration efforts and sage-grouse populations are cyclic with relatively slow growth rates compared with other gallinaceous birds, it may take several breeding cycles before population-level effects due to management actions become noticeable (Garton et al. 2011, Pyke 2011, Messmer et al. 2013). The USFWS will re-evaluate its decision to not list sage-grouse for Endangered Species Act protection as part of a 5-year status review; therefore, more information will be needed to better understand the effects of this management strategy on stabilizing sage-grouse populations.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site. Supporting information includes study area specific information for all seasonal movements. See Supplementary Tables S1–14. Additional Seasonal Movement.