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Research Article

Interseasonal Movements of Greater Sage-Grouse, Migratory Behavior, and an Assessment of the Core Regions Concept in Wyoming

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ABSTRACT Animals can require different habitat types throughout their annual cycles. When considering habitat prioritization, we need to explicitly consider habitat requirements throughout the annual cycle, particularly for species of conservation concern. Understanding annual habitat requirements begins with quantifying how far individuals move across landscapes between key life stages to access required habitats. We quantified individual interseasonal movements for greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) using radio-telemetry spanning the majority of the species distribution in Wyoming. Sage-grouse are currently a candidate for listing under the United States Endangered Species Act and Wyoming is predicted to remain a stronghold for the species. Sage-grouse use distinct seasonal habitats throughout their annual cycle for breeding, brood rearing, and wintering. Average movement distances in Wyoming from nest sites to summer-late brood-rearing locations were 8.1 km (SE = 0.3 km; $n = 828$ individuals) and the average subsequent distances moved from summer sites to winter locations were 17.3 km (SE = 0.5 km; $n = 607$ individuals). Average nest-to-winter movements were 14.4 km (SE = 0.6 km; $n = 434$ individuals). We documented remarkable variation in the extent of movement distances both within and among sites across Wyoming, with some individuals remaining year-round in the same vicinity and others moving over 50 km between life stages. Our results suggest defining any of our populations as migratory or non-migratory is innappropriate as individual strategies vary widely. We compared movement distances of birds marked using Global Positioning System (GPS) and very high frequency (VHF) radio marking techniques and found no evidence that the heavier GPS radios limited movement. Furthermore, we examined the capacity of the sage-grouse core regions concept to capture seasonal locations. As expected, we found the core regions approach, which was developed based on lek data, was generally better at capturing the nesting locations than summer or winter locations. However, across

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Wyoming the sage-grouse breeding core regions still contained a relatively high percentage of summer and winter locations and seem to be a reasonable surrogate for non-breeding habitat when no other information exists. We suggest that conservation efforts for greater sage-grouse implicitly incorporate seasonal habitat needs because of high variation in the amount of overlap among breeding core regions and non-breeding habitat. © 2012 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, core regions, greater sage-grouse, migration, migratory, radio-telemetry, seasonal movements, Wyoming.

Defining and understanding animal-habitat relationships is a fundamental concept in ecology, and the implementation of conservation practices (Boyce and McDonald 1999, Morrison 2001, Brotons et al. 2004). Habitat relationships are often described for animal species during a single season, yet animals typically require different seasonal habitats. The conservation and management of wildlife requires the identification of priority habitat areas that influence all life stages.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a gallinaceous bird limited to western semi-arid sagebrush landscapes (Schroeder et al. 1999). Loss and degradation of native vegetation have affected much of the sagebrush ecosystem and associated wildlife (Knick et al. 2003, Connelly et al. 2004). Sage-grouse have been extirpated from nearly half of their original range in western North America (Schroeder et al. 2004) with range-wide population declines of 45–80% (Connelly et al. 2004). Wyoming contains approximately 37% of the range-wide population, 64% of the population in the eastern range of the species (Doherty et al. 2011), and is predicted to remain a stronghold for sage-grouse populations (Knick et al. 2003).

Sage-grouse require an adequate amount, and juxtaposition of all seasonal habitats for populations to persist (Connelly et al. 2000). Seasonal habitats for sage-grouse are generally considered across 3 life stages: 1) breeding habitat (including lekking, nesting, and early brood-rearing), 2) summer-late brood-rearing habitat, and 3) winter habitat (Connelly et al. 2011). Habitat requirements during these life stages differ in several ways. Generally, nesting and early brood-rearing habitats are characterized by vegetation consisting of greater sagebrush, forb, and grass cover and height (Hagen et al. 2007). Broods move to summer ranges a few weeks post-hatch (Connelly et al. 1988). Hagen et al. (2007) defined the late brood-rearing period as >6 weeks post-hatch and suggested that selection for mesic plant communities with greater herbaceous cover during late brood-rearing reflects a preference for areas with abundant invertebrates and forbs (Johnson and Boyce 1990, Drut et al. 1994). Summer habitats are typically used from July–September, depending on weather conditions (Peterson 1970, Wallestad 1971, Connelly et al. 1988, Gregg et al. 1993, Drut et al. 1994). During winter, sage-grouse rely on sagebrush protruding above the snow for food and shelter (Schroeder et al. 1999). Therefore, snow depth and shrub height are influential components of sage-grouse distributions in winter (Remington and Braun 1985, Homer et al. 1993, Schroeder et al. 1999, Connelly et al. 2000, Crawford et al. 2004). In addition to snow cover, sage-grouse also select for sagebrush and avoid conifers at the landscape scale and avoid riparian areas, conifers, and rugged landscapes at finer scales (Doherty et al. 2008, Carpenter et al. 2010).

Understanding how far sage-grouse move between seasons is required to effectively manage and conserve populations. Recently, multi-scale seasonal habitat selection analyses have been widely used to identify key habitat components and map sage-grouse priority habitats (Aldridge and Boyce 2007; Doherty et al. 2008, 2010; Atamian et al. 2010; Carpenter et al. 2010). A key first step to developing habitat selection models is the determination of biologically meaningful areas that are available to individuals (Jones 2001). Previous sage-grouse studies have assessed movement distances from lek to nesting sites during the breeding season (Holloran and Anderson 2005*b*, Doherty et al. 2010). Thus, we can define available areas during the breeding season based on those distances, realistically capturing what habitats might have been available for animals to use. This information served as the biological foundation for the process of prioritizing the sage-grouse core regions for conservation in Wyoming (Doherty et al. 2011).

However, understanding interseasonal movements among all life stages is necessary to spatially define total seasonal area requirements of populations and to properly manage for connectivity between habitats required to meet all life stages. Doherty et al. (2011) suggested that future work should consider all seasonal habitats when establishing core regions, especially for populations that exhibit long movements to areas outside of breeding habitat—and thereby outside of the delineated core regions—during summer or winter seasons. Previous studies have assessed movement distances from lek to nesting sites (Holloran and Anderson 2005*a*, *b*; Doherty et al. 2010), but few data are available regarding other seasonal movements. Nesting activities occur in close proximity to leks, with approximately 95% of nest sites from 2 extensive studies in Wyoming occurring within 10 km from the lek where the female was captured (Holloran and Anderson 2005*b*, Doherty et al. 2010). Similar movement information is needed between the other sage-grouse life stages: 1) summer-late brood-rearing, and 2) winter. Our primary objective was to use data on seasonal movements of marked birds to quantify the spatial extent of potentially available sage-grouse summer and winter habitats relative to nest and summer habitat. We also examined the influence of radio-marking techniques on movement distances and assesed the capacity of the core regions concept

to capture seasonal locations. We compiled data from 11 sites across Wyoming.

STUDY AREA

We compiled data on sage-grouse movements for 11 study locations from 1998 to 2010 across Wyoming, USA (Fig. 1); a state with a large expanse of sagebrush habitat (approx. 38% of the state; Connelly et al. 2004). These data were collected by many agencies and organizations. In general, each study followed standard capture and monitoring techniques. All study sites were dominated by sagebrush habitats. Details for some study sites can be found in site-specific publications (Holloran et al. 2005, Doherty et al. 2010, Dzialak et al. 2011).

METHODS

Data Compilation

In the context of this manuscript, and throughout, we defined a movement as the distance between paired seasonal telemetry locations for an individual. All birds had to move from 1 location to the next paired location; however, we do not wish to suggest that birds moved directly from 1 location to the next in all observations. Sage-grouse were monitored using very high frequency (VHF) radio necklace collars in 8 studies. Global Positioning System (GPS) transmitters were used to monitor grouse at 3 of the study sites (1 of 2 studies in the Moneta study site, 1 of 2 studies in the Powder River Basin [PRB] study site, and the Jackson study site). In all cases, each individual was assigned a unique identification. The GPS collars provided a large amount of temporal recordings (e.g., up to 1 location every 60 min). Hereafter, we refer to these, respectively, as the VHF and GPS datasets.

All datasets were inspected for quality assurance and quality control (QA–QC) by the individuals and organizations that collected and managed the data. We then compiled all location data, data collection type (e.g., ground, aerial, GPS), and the date associated with each observation. Once

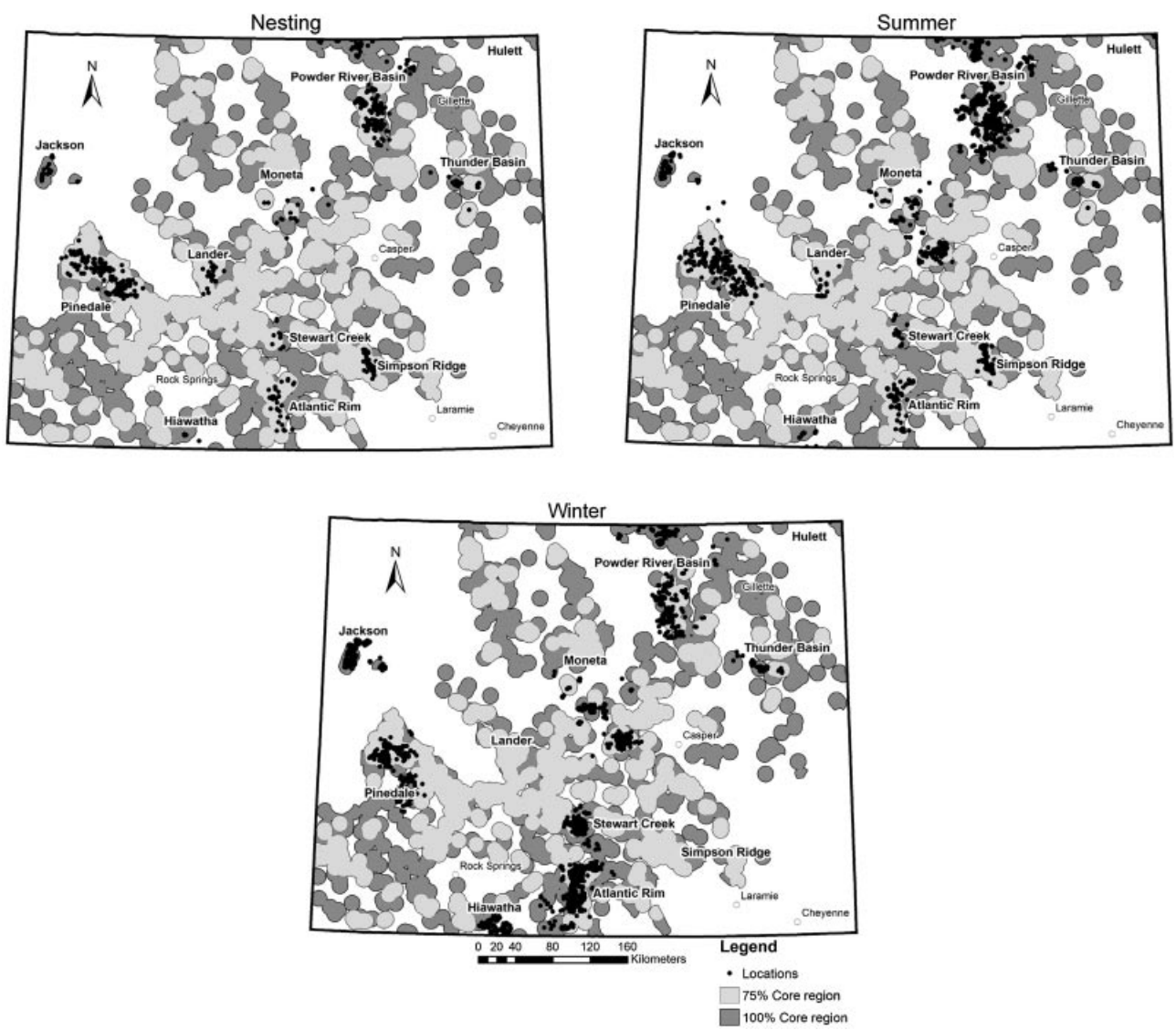

Figure 1. Maps of greater sage-grouse study locations, 1998–2010, Wyoming, USA. The study sites included in our analyses are labeled. Black circles represent seasonal locations. The lighter gray areas represent the estimated 75% core regions. The 75% core regions overlap the darker gray 100% core regions.

the data were compiled, we conducted a second QA–QC, which included an investigation of locational accuracy. When we flagged observations for question (i.e., large individual movements >50 km or data falling in neighboring states or regions), the individuals and organizations that collected the data confirmed or corrected locations through comparison with original data (e.g., field notes). If we could not confirm or correct data, we removed them from the dataset prior to analyses. Removal from the dataset was only required for 1 nest observation and 2 other seasonal observations.

GPS Data Resampling

Because of the large number of GPS locations, we resampled these data to ensure similar contributions relative to VHF datasets. Using VHF datasets, we calculated the number of days between subsequent observations for each unique individual across 2 seasons (late summer and winter). We used these results to inform resampling of the GPS datasets. For each season, we calculated the number of days between subsequent observations for each unique individual in the VHF datasets. We then selected the minimum duration between observations for an individual within a season and year. The mean minimum duration between subsequent observations for each individual in the VHF datasets in summer and winter were 8.6 days (SE = 0.4 days) and 11.4 days (SE = 0.5 days), respectively. These estimates were not substantially different from field objectives. Therefore, we resampled the GPS data with a 7-day interval between subsequent observations to simulate the optimal VHF sampling interval of 1 observation per week. Resampling was not required for nest locations, as nests only occupied 1 location.

The use of GPS radio-transmitters on sage-grouse is a relatively new method. Marking techniques using GPS and VHF transmitters differ in terms of weight and method of attachment. The GPS units are heavier than VHF transmitters, which could be of particular concern in our study as the heavier transmitters may limit movement distances. We examined the possiblility that heavier GPS transmitters limit movement by comparing the distances moved by birds fitted with the 2 transmitter types. The Moneta and PRB study sites were both combinations of 2 independent research studies where 1 study used VHF radio-transmitters and the other used GPS. In both study sites, the studies using different radio-transmitters were in close proximity. For the Moneta study site minimum convex polygons around each study were separated by less than 15 km at their nearest point. The 2 research studies in the PRB study site partially overlapped spatially. If GPS marking techniques limit the movement of individuals, we predicted shorter distances moved by birds marked with GPS transmitters.

Interseasonal Movement Distances

If GPS collars did not limit the movement capabilities of birds, we would combine resampled GPS datasets with VHF datasets to create a single dataset. The peak of nesting activity in Wyoming occurs in May (Holloran 2005). We defined the summer season for birds as 15 June through 31 August each year to capture late summer movements. Birds move from breeding areas as habitats become drier in the late summer. We intended to capture those movements (i.e., to late summer locations). We chose 15 June as the beginning of the late summer season because early-nesting birds could have chicks old enough to make long-distance movements by this date (Schroeder et al. 1999). The winter season included all observations from 1 November through the end of the following February. We calculated the distances moved by sage-grouse from nests to summer locations (nest-to-summer), from summer locations to winter locations (summer-to-winter), and from nests to subsequent winter locations (nest-to-winter). Datasets were dominated by female birds; however, for cases in which data existed for males, we included male movement distances from summer to winter sites. We could not calculate the movement of males from nest sites to summer locations because males do not attend nests. We calculated the maximum distance moved by each individual from 1 season to the next for each year that the individual was observed. To measure nest to summer distances, we calculated the Euclidean distance between the nest site and all subsequent summer locations within that year. A similar approach was used to generate movement distances for each individual's summer location and subsequent winter locations, and nest-to-winter distances. When multiple locations (including multiple nests) for an individual occurred in both seasons, we calculated Euclidean distance for all possible pairwise combinations. From these distances, we retained the maximum Euclidean distance for an individual within a year. If an individual was observed in multiple years, it contributed a distance value for each year. Mortality locations were excluded from analyses because carcasses may have been carried to those locations by predators. Average movement distances can be influenced by age and gender of sage-grouse (Connelly et al. 1988, Leonard et al. 2000, Beck et al. 2006). However, we did not have age or gender information for most of our data and therefore could not analyze the influence of these factors on movement distances.

We quantified how well the sage-grouse core regions captured seasonal locations from our compiled database across Wyoming. To identify core regions Doherty et al. (2011) used an abundance-weighted simple kernel function to delineate priority nesting areas based on proximity of surrounding leks. Breeding density areas were modeled by assigning an abundance-weighted density (based on number of displaying males) to each lek and, starting with the highest density, they summed the number of displaying males until a given percent population threshold was met. This resulted in a defined percent of the sage-grouse breeding population being identified in areas of the highest density of breeding sites. The core region models examined here were groupings of nesting areas that represented the smallest areas necessary to contain 75% (core75) and 100% (core100) of the nesting sage-grouse populations.

We assessed the capacity of the core regions concept to capture interseasonal movements in 2 ways. First, we assessed

the 75% core regions because this is roughly the population threshold that managers have used to delineate sage-grouse priority areas. Several of our study sites were not located within the core75 regions; therefore, we limited the first analysis to those sites that were within in the core75 regions. We selected individual females with nests within the core75 regions. We then determined how many subsequent, non-nesting locations in the summer and winter seasons were also within the core75 boundaries. Our second analysis involved examination of the 100% core regions. These areas represent the known breeding (lek) distribution of sage-grouse in Wyoming. Thus, all of our study sites occurred in the core100 regions. For this analysis we used all location data and summarized, by study site, how many locations were within core100 for each season of interest. All analyses were carried out in STATA version 10.1 (StataCorp LP, College Station, TX). All means are reported with 1 SE.

RESULTS

We separately calculated interseasonal movement distances for the Moneta and PRB study sites for birds marked with VHF and GPS transmitters. For the GPS data, we calculated movement distances using the full data set and the resampled data. Birds marked with GPS transmitters moved farther than birds from the VHF study at the Moneta study site and very similar distances at the PRB study site considering the median values (Table 1). The greater maximum distances moved by the VHF birds in the PRB study site were likely due to the much larger sample of birds, which increases the probability of capturing rare long-distance movements. Therefore, we combined the GPS and VHF datasets for all subsequent analyses. Furthermore, movement estimates from the resampled GPS dataset were similar to movement estimates from the full dataset for both study sites (Table 1).

We calculated interseasonal movement distances from nesting to summer locations and from summer to winter locations. We obtained nest-to-summer movement information for 828 females, resulting in 1,037 individual-by-year distance values. Of these 1,037, movements for 43 females were collected by GPS data and 994 from VHF data. The average distance from nesting to summer locations was 8.1 km (SE = 0.3 km; Table 2, Fig. 2). Of these movement distances, 73% were ≤10 km (range: 41–98%). We obtained summer-to-winter movements for 607 individuals resulting in 752 individual-by-year distance values; 33 were collected from GPS data and 719 from VHF data. The average distance moved from summer-to-winter locations was 17.3 km (SE = 0.5; Table 3, Fig. 2). Of the summer-to-winter movements, 38% were ≤10 km (range: 18–81%). We calculated nest-to-winter movements for 434 individuals resulting in 581 individual-by-year distance values, 21 contributed by GPS data and 560 from VHF data. Average maximum movement distance from nests to winter locations was 14.4 km (SE = 0.6 km; Table 4, Fig. 2). Average proportion of movement distances that were ≤10 km was 50% (range: 35–94%).

The analysis of the core75 regions revealed that 383 birds had nests located within the core, and 72 of those individuals (19%) had at least 1 subsequent seasonal location that was outside of the core75 regions. The 383 birds with nests in core75 provided 1,667 locations in the summer (n = 1,401) and winter (n = 266) seasons. In the summer season, 85% of the locations (n = 1,186) fell within the core75 boundaries. For winter, 65% of the locations (n = 174) occurred within the core75 boundaries. The pattern of decreasing proportion of locations within core regions across seasons was similar when we analyzed the core100 regions. Across all sites the average number of nest locations within core100 regeions

Table 1. Interseasonal movement distances (km) for sage-grouse from 2 study sites (Moneta, Powder River Basin). Distances calculated from nest site location to summer locations (nest–summer), summer locations to winter locations (summer–winter), and nest site location to winter locations (nest–winter) 2003–2010, Wyoming, USA. We analyzed 3 datasets for each study site. The first data sets contained only birds marked with very high frequency (VHF) radio-transmitters. The second datasets included all observations of birds marked with Global Positioning System (GPS) transmitters. The third data sets were the GPS dataset resampled to an observation frequency similar to the VHF dataset. All Observations were the maximum distance moved by an individual within a year. Reported statistics include: n = number of observations per site; p5 = 5th percentile; p90 = 90th percentile; and p95 = 95th percentile; pairwise comparisons = the number of pairwise distances calculated for each dataset.

Study site	Seasons	Dataset	n	Mean	SE	Median	Min.	Max.	p5	p90	p95	Pairwise comparisons
Moneta	Nest–summer	VHF	30	4.69	0.68	3.65	0.02	18.29	1.02	9.10	11.68	215
		GPS—full	13	9.82	2.04	7.29	0.99	22.57	0.99	18.81	22.57	9,519
		GPS—resampled	13	9.31	2.14	5.21	0.89	22.34	0.89	18.73	22.34	130
	Summer–winter	VHF	112	9.70	0.47	8.67	1.95	23.40	2.92	16.87	19.23	1,887
		GPS—full	13	21.18	2.45	20.98	7.70	34.43	7.70	32.52	34.43	889,080
		GPS—resampled	13	19.15	2.62	19.55	5.51	34.16	5.51	31.22	34.16	1,138
	Nest–winter	VHF	24	9.21	0.92	8.67	3.51	18.61	3.71	15.47	15.97	120
		GPS—full	6	12.55	4.31	8.77	3.64	31.23	3.64	31.23	31.23	886
		GPS—resampled	6	11.32	4.26	7.13	3.35	30.20	3.35	30.20	30.20	47
Powder River Basin (PRB)	Nest–summer	VHF	425	8.05	0.40	5.49	0.05	51.76	1.25	18.79	26.60	4,712
		GPS—full	22	6.70	1.36	5.30	0.87	25.97	1.35	15.17	20.77	15,494
		GPS—resampled	22	6.09	1.37	4.45	0.65	25.94	1.20	13.59	20.76	214
	Summer–winter	VHF	183	11.35	0.70	7.87	1.48	50.49	2.52	24.91	31.99	4,099
		GPS—full	14	11.83	1.68	9.69	2.98	23.91	2.98	22.72	23.91	1,019,421
		GPS—resampled	14	9.94	1.73	7.06	1.99	22.66	1.99	21.53	22.66	1,190
	Nest–winter	VHF	163	9.46	0.73	5.66	0.09	39.25	0.83	24.88	30.29	294
		GPS—full	12	7.30	1.11	7.71	2.13	12.05	2.13	11.26	12.05	1,862
		GPS—resampled	12	6.28	1.01	6.69	1.17	10.31	1.17	10.30	10.31	91

Table 2. Interseasonal movement distances (km) for female sage-grouse from nest site location to summer locations, 1998–2009, Wyoming, USA. Observations were the maximum distance moved by an individual within a year. Reported statistics include: n = number of observations per site; p5 = 5th percentile; p90 = 90th percentile; and p95 = 95th percentile.

Study site	n	Mean	SE	Median	Min.	Max.	p5	p90	p95
Atlantic Rim	42	6.04	0.85	4.35	0.01	23.64	0.22	14.16	17.66
Hiawatha	13	5.41	1.27	5.60	0.15	12.99	0.15	12.04	12.99
Hulett	11	10.15	3.67	3.20	0.67	32.27	0.67	32.15	32.27
Jackson	36	5.62	0.92	3.39	0.90	24.84	1.06	10.66	22.35
Lander	41	14.35	1.65	12.51	0.87	34.72	1.10	29.89	31.53
Lysite	15	10.23	2.10	8.13	0.89	24.35	0.89	22.34	24.35
PRB[a]	447	7.96	0.38	5.44	0.05	51.76	1.21	18.79	26.37
Pinedale	335	8.84	0.48	5.83	0.00	57.75	0.90	18.60	24.56
Simpson Ridge	43	4.31	0.78	2.65	0.75	27.05	0.82	7.62	14.16
Stewart Creek	12	10.11	2.62	7.69	1.31	33.23	1.31	18.78	33.23
Thunder Basin	41	3.81	0.75	2.61	0.17	30.79	0.55	6.18	7.21
Total	1,036	8.07	0.26	5.28	0.00	57.75	0.93	19.04	25.94

[a] Powder River Basin.

was 92% (SE = 4%, range: 65–100%). Average number of summer locations within core100 was very similar (91%, SE = 4%, range: 62–100%). However, the average number of winter locations within the core100 was lower at 78% (SE = 7%) and had a much broader range among study sites from 31% to 100%.

DISCUSSION

Sage-grouse in Wyoming make substantial movements between critical life stages. Interseasonal movements have been documented for sage-grouse in several individual studies across the sage-grouse range. Our research represents the largest spatial extent examined to date, allowing for a more robust determination of biologically meaningful seasonal habitats available to sage-grouse. Furthermore, our research addresses the definition of the migratory status of populations, the influence of GPS radio-transmitters, and provides an assessment of the core regions concept.

Our interseasonal movement distance results are similar to those presented in other studies, allowing generalizations about potential areas of interest among interseasonal habitats. However, we documented substantial variation in interseasonal movement distances among study sites and among individuals within study sites across all life stages (Tables 2–4). This variation highlights the uniqueness of populations and that the capacity of individuals in these populations to access suitable seasonal habitats varies depending on landscape composition (study site). For example, the PRB and Thunder Basin sites are adjacent to each other and share similar geography (Fig. 1). However, birds in the PRB tended to move farther on average (nesting-to-summer $\bar{x}$ = 8.0 km, summer-to-winter $\bar{x}$ = 11.3 km, nest-to-winter $\bar{x}$ = 18.5 km) than birds in Thunder Basin (respectively; $\bar{x}$ = 3.8 km, $\bar{x}$ = 7.1 km, and $\bar{x}$ = 5.6 km; Tables 2 and 3). Thus, results from 1 area may not necessarily apply to others and may be related to levels of fragmentation and overall habitat availability. However, we have captured an extensive geographic distribution of sage-grouse and these distances can serve as a foundation when developing future research projects; particularly those focused on developing habitat selection models which require a clear definition of the habitats available to an animal (Jones 2001).

Movement distances may be affected by annual variation in moisture availability. In wet years, birds may not need to move as far to find mesic sites (Aldridge 2000). Fischer et al. (1996) reported that birds moved to late brood-rearing sites when vegetation moisture declined to approximately 60%, and seasonal movements were intiated earlier in drier years. In eastern Idaho, Klebenow and Gray (1968) observed an upward shift in elevation with grouse moving 8–24 km to summer ranges; these distances are very similar to the distances we report. In Montana, movement distances to late brood-rearing habitats were relatively short (5 km; Wallestad 1971). Bird movement distances may also be influenced by tradition, with individuals bypassing apparently comparable sites that are closer (Wallestad 1971). Fidelity to winter locations has also been demonstrated for sage-grouse (Berry and Eng 1985, Schroeder et al. 1999), and may influence movement to winter areas from late brood-rearing areas. Our maximum recorded movement distance from late brood-rearing to winter habitat was 83 km (Pinedale study site), a distance somewhat less than the 80–160 km reported for the upper Green River Basin, Wyoming (Patterson 1952). Likewise, maximum movement distance from nest to late brood-rearing habitats reported for populations in southeatern Idaho were 82 km (Connelly et al. 1988), which exceeded the maximum distance for any of our Wyoming study sites.

Sage-grouse habitat use is influenced by landscape-scale factors (Doherty et al. 2008). The scale of interseasonal movement distances presented here supports previous work describing the landscape nature of the species. Based on our distance measures, a population may require entire landscapes to encompass the seasonal habitats required by the population. Because we are studying a species of conservation concern, we considered the 90th percentile of the measured movement distances of sage-grouse in Wyoming appropriate for consideration of what area constitutes the potential landscape available to a population. Overall, for Wyoming, the 90th percentile involves 19-km movements from nest to late summer and (potentially) an additional

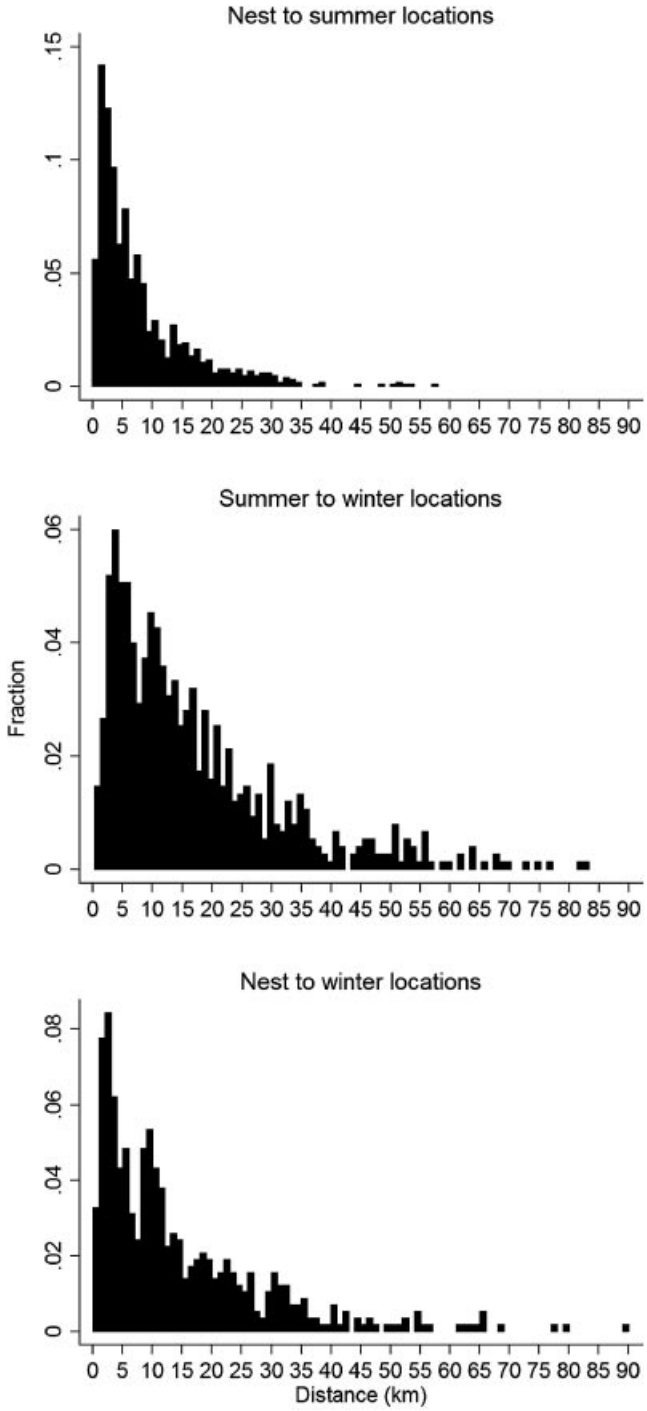

Figure 2. Histograms depicting the average distances moved by individual greater sage-grouse between seasons, Wyoming, USA. Nest to summer data were collected between 1998 and 2010 and movements to winter locations were collected from 2001 to 2010. The *y*-axis is scaled such that the height of each bar is the probability of falling within the range of *x*-values represented by the bar (fraction of values). Bar widths are in 1-km groupings.

36 km from late summer to winter locations. The data included in these analyses are from sage-grouse in the core of the species' range, including relatively unfragmented habitats. The extent required by an individual to meet annual resource requirements from populations in more fragmented landscapes may be considerably larger (Hagen et al. 2001). Furthermore, greater movement distances may have a negative impact on the survival of juvenile birds (Beck et al. 2006). In addition to landscape configuration, age and gender can influence movement distances. Previous research suggests that for some interseasonal movements, juveniles will move farther than adults (Connelly et al. 1988) and males may tend to move farther that females (Beck et al. 2006). The majority of our data were for adult females; therefore, our estimates should likely be considered minimum estimates.

The interseasonal movements of sage-grouse have been used to classify populations into 4 categories of migratory behavior. The classifications are: 1) resident, 2) 2-stage winter migratory (from a breeding and summer area to a winter area), 3) 2-stage summer migratory (from a winter and breeding area to a summer area), or 4) 3-stage migratory (between separate breeding, summer, and winter areas; Connelly et al. 2004). In our analysis, substantial overlap of all seasonal points generally existed within each study site, with the possible exception of the Atlantic Rim, Pinedale, and Stewart Creek study sites (Fig. 1). Indeed, the Atlantic Rim and Pinedale study sites are fairly unique with mean summer-to-winter movement distances almost twice as large (23 km) as the other study sites. The broad-scale analyses presented here are not of sufficient detail to classify the migratory behavior of our study sites (populations). Furthermore, our results suggest remarkable variation in the extent of movement distances both within and among sites across Wyoming, with some individuals remaining year-round in the same vicinity and others moving over 50 km between life stages. These findings suggest that individuals can use different migratory strategies within the same population. Connelly et al. (2000) suggested a population should be considered non-migratory if indivduals make movements <10 km. The proportion of maximum interseasonal movement distances that were <10 km vary widely across seasons and study sites. The average proportion of summer-to-winter movements 10 km was 38%. Therefore, assigning a particular migratory classification to an entire population (study site) is difficult. Individuals within a population are clearly pursuing different migratory strategies to fulfill their annual habitat requirements.

The GPS radio-transmitters did not seem to limit interseasonal movement distances. However, we could not assess the influence of transmitter type on fitness components such as survival, predation, or reproductive success. We suggest that future research addressing such issues is necessary to fully understand the effects of different transmitter types. Also of note, the movement distances estimated from the resampled GPS data sets were equivalent to the movement distances from the full GPS datasets. Thus, for the purposes of estimating seasonal movement distances, 1 observation per week is likely sufficient to capture variation in an individual's movement behavior.

MANAGEMENT IMPLICATIONS

Sage-grouse across Wyoming may move substantial distances between seasonal habitats. Therefore, conservation

Table 3. Interseasonal movement distances (km) for female and male sage-grouse from summer to winter locations, 2001–2010, Wyoming, USA. Observations were the maximum distance moved by an individual within a year. Reported statistics include: n = number of observations per site; p5 = 5th percentile; p90 = 90th percentile; and p95 = 95th percentile.

Study site	*n*	Mean	SE	Median	Min.	Max.	p5	p90	p95
Atlantic Rim	120	23.29	1.68	18.71	0.67	82.19	1.72	52.87	60.90
Hiawatha	28	9.08	0.78	9.73	1.08	16.01	3.28	15.13	15.46
Hulett	2	13.87	5.38	13.87	8.49	19.25	8.49	19.25	19.25
Jackson	37	13.75	1.13	12.83	2.11	34.79	3.78	21.28	29.48
Lysite	65	10.87	0.93	8.94	2.44	34.16	2.92	20.37	25.48
PRB[a]	197	11.25	0.66	7.84	1.48	50.49	2.50	24.79	31.99
Pinedale	249	23.79	1.05	20.44	0.33	83.32	3.05	47.78	55.61
Stewart Creek	28	13.26	1.43	11.85	2.67	29.73	2.80	26.07	28.92
Thunder Basin	26	7.10	1.22	5.00	1.91	31.09	1.93	13.25	18.95
Total	752	17.27	0.54	13.01	0.33	83.32	2.54	36.14	50.49

[a] Powder River Basin.

Table 4. Interseasonal movement distances (km) for female sage-grouse from nest to winter locations, 2001–2009, Wyoming, USA. Observations were the maximum distance moved by an individual within a year. Reported statistics include: n = number of observations per site; p5 = 5th percentile; p90 = 90th percentile; and p95 = 95th percentile.

Study site	*n*	Mean	SE	Median	Min.	Max.	p5	p90	p95
Atlantic Rim	30	18.76	3.74	10.72	1.09	80.02	1.19	51.16	61.44
Hiawatha	14	5.81	1.15	4.17	1.02	14.15	1.02	13.40	14.15
Jackson	29	12.16	1.30	11.81	1.40	34.72	2.38	21.92	24.97
Lysite	6	11.32	4.26	7.13	3.35	30.20	3.35	30.20	30.20
Pinedale	175	9.24	0.69	5.90	0.09	39.25	0.83	23.37	30.29
PRB[a]	298	18.54	0.90	14.10	0.23	89.67	1.88	40.12	52.34
Stewart Creek	11	7.61	1.60	7.46	1.72	19.90	1.72	13.18	19.90
Thunder Basin	18	5.63	1.55	4.02	1.34	30.53	1.34	9.02	30.53
Total	581	14.44	0.59	10.04	0.09	89.67	1.27	32.50	42.28

[a] Powder River Basin.

efforts focused soley on sage-grouse breeding areas will not likely capture all annual sage-grouse needs (Aldridge and Boyce 2007, Doherty et al. 2011) unless leks are also present in the other seasonal habitats. Sage-grouse breeding core regions contained a relatively high percentage of summer and winter locations on average and may be a reasonable surrogate for non-breeding habitat when no other information exists. However, in some populations overlap between breeding core regions and other seasonal habitat was low. For example, in the Hiawatha study site, only 31% of winter locations were within the 100% breeding core. Therefore, we concur with Doherty et al. (2011) that broadening the scope of the sage-grouse core regions to include other habitats used by sage-grouse that may not be currently represented in the core region approach will increase the biological rigor of conservation efforts. The development and use of state-wide seasonally explicit habitat selection models would more accurately identify and delineate suitable seasonal habitats. We suggest the use of seasonally explicit habitat selection models combined with site-specific information will allow the strategic targeting of areas used by individuals whose breeding habitats are protected by currently described core regions. The scale of movements also illustrates that future work will require the identification of corridors that connect high priority seasonal habitats, both within and among populations.

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