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Ecology of greater sage-grouse populations inhabiting the northwestern Wyoming Basin

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Abstract: Range-wide population declines of greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) have been largely attributed to habitat loss and fragmentation. However, the specific conservation threats affecting the ecology of sage-grouse populations may differ by region. Although the status of the Bear Lake Plateau and Valley (BLPV) sage-grouse populations in the Wyoming Basin has been monitored using male lek counts since the 1960s, little was known about their ecology, seasonal movements, and habitat use patterns. From 2010–2012, we radio-marked 153 sage-grouse (59 females and 94 males) with very high frequency necklace-style radio-collars throughout the BLPV study area, which encompassed parts of Bear Lake County, Idaho, and Rich County, Utah. We subsequently monitored the radio-marked sage-grouse to estimate the factors affecting vital rates, seasonal movements, and habitat use. Radio-marked sage-grouse primarily used seasonal habitats in Idaho and Utah, but some individuals used seasonal habitats in Wyoming. The average annual survival rate for the radio-marked sage-grouse was 53% (±3%). Average female nest success (23%; 95% CI = 18–29%) was lower than range-wide estimates. Brood success varied between 2011 and 2012, with higher brood survival observed in 2012. Twenty-four percent of radio-marked sage-grouse were migratory, engaging in seasonal movements ≥10 km. Annual home range estimates using kernel density estimator (101 km^2) for radio-marked sage-grouse were within estimates previously reported. However, poor recruitment attributed to low nest and brood survival may be impacting overall population stability. Because the radio-marked sage-grouse used seasonal habitats in 3 states, we recommend that Utah, Idaho, and Wyoming coordinate in the development of a tri-state management plan to better conserve this population.

Key words: Bear Lake Plateau and Valley, *Centrocercus urophasianus*, fragmentation, greater sage-grouse, habitat management, Idaho, Utah, vital rates

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) are a sagebrush (*Artemisia* spp.) obligate species that are estimated to currently occupy about 668,412 km^2 or <60% of their pre-settlement range (Schroeder et al. 2004). Declines in sage-grouse populations have mainly been attributed to sagebrush ecosystem loss and degradation (Connelly et al. 2004, Knick and Connelly 2011). In response to population declines, the species was designated by the U.S. Fish and Wildlife Service (USFWS) in 2010 as a candidate for protection under the Endangered Species Act (ESA) of 1973 (USFWS 2010). However, in 2015, USFWS determined that the species did not warrant ESA protection because range-wide conservation efforts had mitigated species conservation threats for >90% of the range-wide population (USFWS 2015).

Sage-grouse require large expanses of sagebrush to meet all of their seasonal habitat requirements (Connelly et al. 1988, Hagen 1999, Connelly et al. 2000*a*). Thus, the movement and dispersal of radio-marked individuals is a useful measure of the effects of anthropogenic and natural habitat fragmentation on populations (Wiens 1994, Fedy et al. 2012, Dahlgren et al. 2016*a*, *b*). Habitat loss and fragmentation could affect seasonal ranges and alter movement patterns by creating movement barriers between populations (Knick et al. 2013). Range reduction, fragmentation, and isolation may reduce connectivity among populations, leading to loss of genetic diversity and population decline due to natural disasters (Reese and Connelly 1997, Benedict et al. 2003, Oyler-McCance et al. 2005, Aldridge et al. 2008).

The USFWS (2013) emphasized the need to focus conservation efforts on protecting and enhancing priority sage-grouse habitats because they afford increased certainty that conservation actions will result in population persistence (Stiver et al. 2006, USFWS 2013).

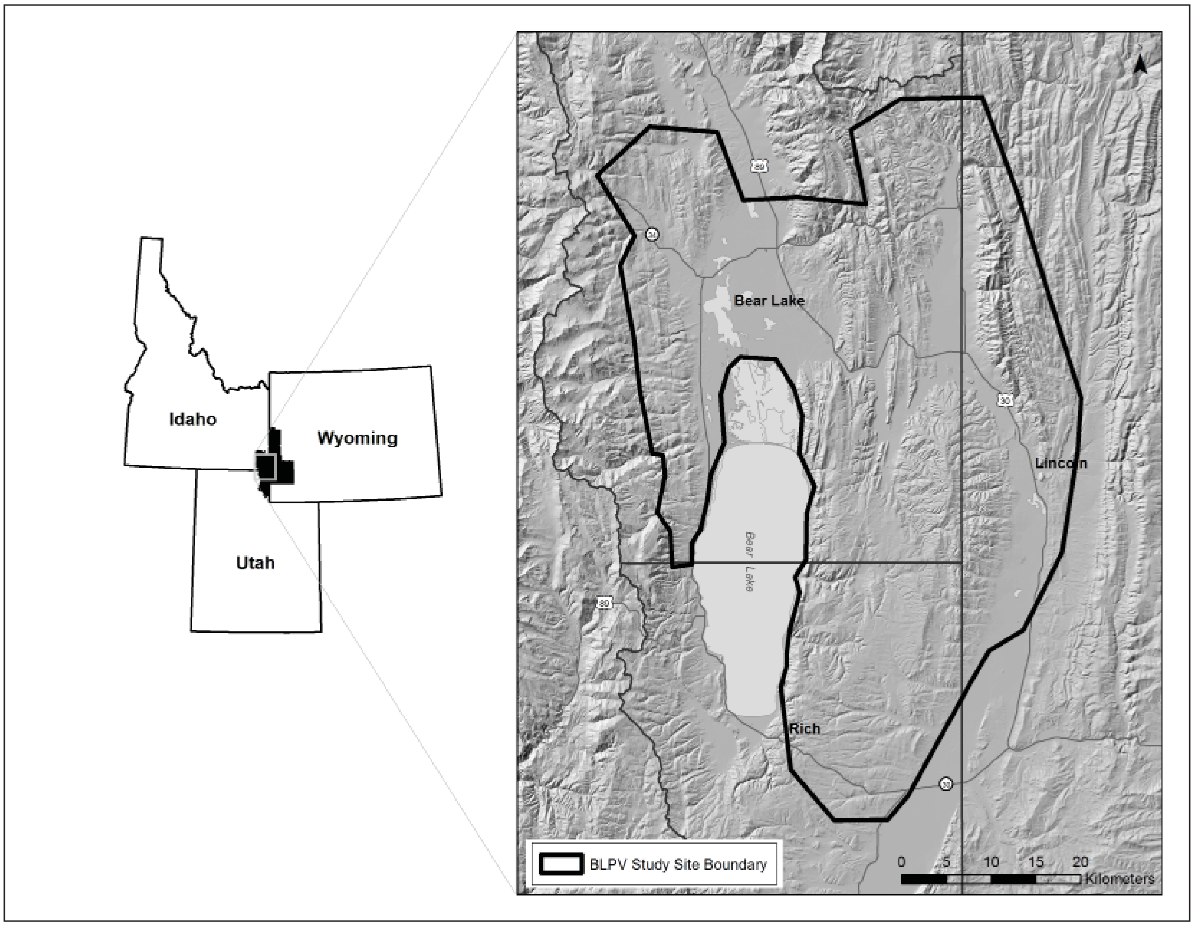

Figure 1. Bear Lake Plateau and Valley (BLPV) study area, Idaho-Utah-Wyoming, USA. Area included 99% of all recorded greater sage-grouse (*Centrocercus urophasianus*) locations, 2010–2012.

Sage-grouse conservation planning within state and federal agencies has embraced strategic landscape management approaches (Idaho Department of Fish and Game 2006, Utah Division of Wildlife Resources 2013, U.S. Department of Interior 2015). However, most state and federal conservation planning efforts still focus on the application of conservation strategies within state or jurisdictional boundaries. Management of sage-grouse may be further complicated because of the mosaic of private and public landownership (Messmer 2013).

Sage-grouse populations may use distinct seasonal ranges, which often transcend jurisdictional boundaries (Reinhart et al. 2013, Cardinal 2015, Dahlgren et al. 2016*a*). The size of these seasonal ranges may reflect historical land uses working in concert with spatial habitat needs (Messmer 2013, Dahlgren et al. 2016*a*). Better information regarding sage-grouse seasonal movement and mitigation is needed to determine meta-population boundaries, identify important seasonal habitats, and define how the birds respond to changes in land use (Connelly et al. 1988, Fedy et al. 2012, Messmer 2013, Dahlgren et al. 2016*a*). This is important because a strong relationship exists among movement patterns, survival, and productivity (Beck et al. 2006, Connelly et al. 2011*a*). Additionally, better information about the ecology of unstudied populations could be important for management of sage-grouse populations, especially for populations that span >1 jurisdictional boundary. For these populations, achieving conservation will require increased coordination among multiple agencies, landowners, and the public (Hemker and Braun 2001, Messmer 2013, Rienhart et al. 2013).

Little is known about the ecology, seasonal movements, and habitat use patterns of the sage-grouse populations that inhabit the Bear Lake Plateau and Valley (BLPV) relative to existing or potential land uses for application to management. Our objective was to describe the ecology, seasonal movements, and habitat use patterns of sage-grouse that inhabit the BLPV relative to existing land uses and jurisdictional boundaries. This information will be important to identify conservation strategies and implement management actions to conserve these meta-populations (USFWS 2013).

Study area

The BLPV is located in Bear Lake County, Idaho, Rich County, Utah, and Lincoln County, Wyoming (Figure 1). The BLPV study area encompasses 2,450 km^2 and constitutes the northwestern portion of the Wyoming Basin (Stiver et al. 2006). Approximately 58% of the area was privately owned, 9% state-owned land, 8% managed by the U.S. Forest Service (USFS), 24% managed by the Bureau of Land Management (BLM), and 1% managed by the USFWS. The elevation of the study area ranged from 1,800–2,500 m above sea level. The BLPV consists of north-south sagebrush-steppe plateaus that parallel one another. The dominant shrubs included Wyoming big sagebrush (*A. tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), basin big sagebrush (*A. t. tridentata*), black sagebrush (*A. nova*), serviceberry (*Amelanchier utahensis*), snowberry (*Symphoricarpos* spp.), and rabbitbrush (*Chrysothamnus* spp.). Common grasses included wheatgrasses (*Agropyron* and *Pseudoroegneria* spp.), bromegrass (*Bromus* spp.), bluegrass (*Poa* spp.), and wild rye (*Elymus* spp.). Common forbs included: *Phlox* spp., redtop (*Agoseris glauca*), hawksbeard (*Crepis acuminata)*, groundsel (*Baccharis salicina*), rosy pussytoes (*Antennaria rosea*), milk vetch (*Astragalus* spp.), penstemon (*Penstemon* spp.), and daisy (*Erigeron* spp.). In Idaho, Caribou National Forest borders the BLPV on the west side and on the north edge of the valley. In Utah, Cache National Forest borders the BLPV on the west side. The Cache and Caribou National Forests are characterized by high-elevation tree stands consisting of lodgepole pine (*Pinus contorta*), spruce (*Picea* spp.), fir (*Abies* spp.), and aspen (*Populus tremuloides*), and sagebrush-steppe in lower elevations (O'Brien and Pope 1997).

The climate of the BLPV study area is typical of intermountain highlands with cold winters and hot summers. Temperatures range from average lows of -14°C in January and highs of 29°C in July. The area receives 25–43 cm of precipitation annually, most of which occurs between September and June as snow in the winter and rain in the summer. The average annual snowfall varies through the site varying 83–235 cm, and most of this occurs from October to March (Western Regional Climate Center 2013).

The primary land use was grazing by domestic livestock. Because of the presence of Bear Lake, the BLPV is also a major seasonal recreation area, with most use occurring from May to September. Residential development is occurring at the base of Bear Lake on both the east and west sides of the study area. On the BLPV plateau west of Bloomington, Idaho, a mining corporation has been exploring for phosphate.

Personnel with the Idaho Department of Fish and Game (IDFG), Utah Division of Wildlife Resources (UDWR), and Wyoming Game and Fish Department (WGFD) have monitored sage-grouse leks in the area since the 1960s. However, not all leks are counted each year, but rather every few years; state agencies conduct aerial surveys to census all leks (J. Connelly, IDFG, personal communication).

Methods

Radio-telemetry

The sage-grouse we studied were captured and radio-marked near known leks and roost sites throughout the study area in the spring and fall from March 2010 to April 2012. We used spotlights and binoculars to locate roosting sage-grouse and dip nets to capture them (Wakkinen et al. 1992*b*, Connelly et al. 2003). We used all-terrain vehicles and foot-capture methods, as rough terrain limited the use of larger vehicles. Sage-grouse were classified by sex (male or female) and age (juvenile, yearling, or adult) using size and plumage (Beck et al. 1975). Females and males were fitted with individually numbered leg bands, and 18–26-g necklace-style very high frequency (VHF) radio-transmitters (Advanced Telemetry Systems, Isanti, MN, USA; American Wildlife Enterprises, Monticello, FL, USA; Wildlife Materials, Murphysboro, IL, USA; Sirtrack, Havelock North, New Zealand). All captured sage-grouse were handled according to procedures approved under the Utah State University (USU) Institutional Animal Care and Use Committee Permit #1463, and with a Certificate of Registration from the UDWR #3BAND8430, and a Wildlife Collection Permit from IDFG, #100419.

The VHF radio-transmitters deployed on sage-grouse were equipped with an 8-hour mortality sensor. When a mortality signal was detected, the collar was located and the cause of mortality was determined by examining carcass and remains. We evaluated survival by year, sex, area of capture, and migratory status (Beck et al. 2006, Caudill et al. 2016).

Nesting

Radio-marked females were located using telemetry ≥1 times per week from April to August. We used caution not to flush the nesting female because of the risk of nest abandonment (Connelly et al. 2011*a*). We considered a female to be nesting when it was located under the same bush for 3 consecutive days. Nest locations were inconspicuously marked using small rock piles placed ≥30 m in a cardinal direction from the nest bowl and the Global Position System (GPS) location recorded. Nest fate was determined by monitoring incubation time and locating nest remains after success or failure. Successful nests had ≥1 eggshells with loose membranes present (Girard 1939).

Nest site vegetation

Nest vegetation was measured after nest fate was determined. Random points within 5 km of each nest were selected using Geographic Information System (GIS) technology (ArcMap GIS 10.1 program), and vegetation measurements were taken to compare selection of available nesting habitat in the study area (Connelly et al. 2003). Aspect and slope were recorded at each nest and random site. From the nest bowl or random Universal Transverse Mercator (UTM) point, a 15-m intercept transect was established with an initial random compass bearing, and ≥3 transects were established at 90° angles to measure shrub cover (Canfield 1941). Along these transects, we measured herbaceous cover every 3 m using Daubenmire frames (40 cm x 25 cm; Daubenmire 1959). We used a Robel pole (Robel et al. 1970) to measure vegetation visual cover or obstruction (VOR). The VOR was recorded at 5 m from the nest bowl location along each transect at 100 cm high, looking into and out from the Robel pole.

Brood monitoring

We approached females with broods during the day on foot or were spotlighted at night to observe chicks (Dahlgren et al. 2010). Broods were not flushed more than once a week to avoid distress to the chicks. A female was considered to have produced a successful brood if at least 1 chick survived >50 days (Schroeder 1997).

Brood site vegetation

When we located a brood, we recorded a GPS location and measured vegetation at that site within 5–7 days. At brood sites, vegetation was measured along a 10-m line-intercept transect at a random compass bearing, and then at 3 subsequent 90° angles. We used Daubenmire frames (40 cm x 25 cm; Daubenmire 1959) to measure ground cover (percent grass, forb, bare ground, litter, and rock) every 2.5 m along the line-intercept transects. The VOR was recorded at 5 m from the brood site along each transect at 100 cm high. Aspect and slope were recorded at each site. Random points within 5 km of each brood were selected in GIS, and vegetation measurements were taken to compare selected habitats to potential habitat (Connelly et al. 2003).

Movements

All sage-grouse spatial locations were recorded using the geographic coordinate system Universal Transverse Mercator (UTM) Zone 12 T. We located ≥1 radio-marked sage-grouse per week during spring and summer (March 15 to September 15), ≥1 per month during fall (September 15 to December 15), and ≥1 per winter (December 15 to March 15). We used ground telemetry to triangulate locations of sage-grouse during spring, summer, and fall. We used aerial telemetry from a fixed-wing aircraft to obtain locations when the site was inaccessible or if birds were missing. When sage-grouse were flushed, a GPS location and the number of birds present were recorded.

Home range

We calculated home range size for individual radio-marked sage-grouse. Individuals that

Table 1. Models assessing the impact of temporal and habitat factors on survival of greater sage-grouse (*Centrocercus urophasianus*), Bear Lake Plateau and Valley study area, Idaho-Utah, USA, 2011–2012.

Model	K[a]	AICc[b]	Δ AICc[c]	*w* [d]
Season + Capture area	8	314.71	0.00	0.51
Capture area + Individual year	5	316.37	1.66	0.22
Capture area	4	318.83	4.12	0.07
Season + Age	8	319.30	4.58	0.05
Season	7	319.72	5.01	0.04
Season + Individual year	5	320.78	6.07	0.02
Season + Sex	3	321.10	6.38	0.02
Year	5	321.54	6.83	0.02
Age	2	323.13	8.41	0.01
Age + Individual year	5	323.52	8.80	0.01
Individual year	4	323.58	8.87	0.01
Null	1	323.97	9.26	0.01
Year (continuous)	2	324.17	9.46	0.00
Sex + Age	5	324.69	9.98	0.00
Sex + Individual year	5	325.06	10.34	0.00
Sex	2	325.28	10.56	0.00

[a] K: number of parameters in each model
[b] AICc: Akaike Information Criterion corrected for small sample size
[c] Δ AICc: difference between a model and the best performing model
[d] *w*: Akaike model weight

had <10 locations recorded were removed from analysis because of inadequate sample size (Rudeen 2012). Only 1 GPS location was used for nesting females in home range estimations. For comparison to other studies, we used the kernel density estimator (KDE) in GME (Geospatial Modelling Environment, GME 0.7.2.1; Beyer 2012), minimum convex polygon (MCP) estimates in GME, and local convex hull (LoCoH; Getz and Wilmers 2004) in Program R (R Development Core Team 2012). We calculated a KDE using Least Square Cross Validation for the algorithm (Lichti and Swihart 2011), a cell size of 10, and the default scaling factor of 1,000,000 (Sheather and Jones 1991, Seaman et al. 1999, Lichti and Swihart 2011). Isopleths representing probability surfaces were created to contain 95% of the volume of the KDE raster surface using GME (GME 0.7.2.1). LoCoH utilization distributions were estimated at 100.1%, which encompassed a greater amount of area in the case that points used did not fully capture the true utilization distribution. MCP home ranges were calculated using 100% of each individual's points.

Data analysis

The ragged telemetry data were best suited for estimating seasonal survival rates using the nest survival model in program MARK (White and Burnham 1999), which allowed for use of staggered entry and irregular monitoring (Johnson 1979, Dinsmore et al. 2002, Rotella et al. 2004). Survival was assessed with season as the time interval, and sage-grouse that survived from >1 year were re-entered into the model as separate individuals. Covariates that were assessed for an effect on survival included sex, age, year, season, and capture area. We used the R (R Development Core Team 2012) package RMark (Laake and Rexstad 2013) to construct nest survival models for program MARK (White and Burnham 1999). We ranked competing models using Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). When there were multiple top competing models (ΔAICc ≤ 2), models with uninformative parameters were removed, and the model with the lowest number of parameters was retained for interpretation (Arnold 2010). The 95% confidence intervals (CI) and variance for survival was calculated using the delta method (Seber 1982).

We analyzed nest success using the nest survival model using R (R Development Core Team 2012), package RMark (Laake and Rexstad 2013), to construct models for program MARK (White and Burnham 1999), which allowed for use of ragged monitoring data (Johnson 1979, Dinsmore et al. 2002, Rotella et al. 2004). The nest survival model calculates daily survival rates, which can then be combined to estimate nest survival. Nest success was calculated by daily survival rate raised to the power of total combined nest laying and incubation time period (36 days). Nest success confidence intervals were calculated using the delta method (Seber 1982). Covariates used to analyze nest success included aspect, slope, percent big sagebrush cover, average sagebrush height, percent forb cover, average forb height, percent grass cover, average grass height, distance to nearest fence, distance to nearest road, and distance to nearest anthropomorphic structure. We evaluated the effect of covariates on nest success using RMark. We ranked competing models using Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). When there were multiple top competing models (ΔAICc $\leq$ 2), models with uninformative parameters were removed, and the model with the lowest number of parameters was retained for interpretation (Arnold 2010).

We compared vegetation differences between successful and unsuccessful nests using AICc model selection in RMark. Habitat characteristics including nest shrub height and diameter; cover and heights of shrubs, forbs, and grasses; and percentages of bare ground, litter, and rock were assessed for impact on nest success. We also measured vegetation at random locations and analyzed it for differences from nest site vegetation using logistic regression (PROC LOGISTIC, SAS® System for Windows 9.3, Cary, NC, USA). The random points were selected in areas within 5 km of a lek and were located within potential nesting cover. Habitat characteristics were compared at distances of 3, 6, 9, and 12 m from the site.

Because of low sample sizes, descriptive statistics were used to describe brood success. We analyzed brood selection vegetation variables using logistic regression (PROC LOGISTIC, SAS). All habitat characteristics, including height and percent cover of shrubs, forbs, and grasses, and percent of bare ground, litter, and rock were assessed for impact on brood site selection. Habitat characteristics were compared for differences at 2.5, 5, 7.5, and 10 m from the brood and random sites.

All sage-grouse spatial locations were downloaded into GIS and were transformed into shapefiles. We assessed each location shapefile in GIS to determine if the individual was migratory and to determine a distance between each seasonal range. Individuals that moved ≥10 km between seasonal-use ranges were considered migratory (Connelly et al. 2011*a*). Individuals that did not survive multiple seasons were classified as undetermined, as distances moved by individuals between seasonal ranges could not be accurately defined (Fedy et al. 2012, Reinhart et al. 2013). We used the GPS location data to assess distance of nest from nearest lek and capture lek and distance from each brood site to nest site. Differences in estimated home range size were assessed using a *t*-test (PROC TTEST, SAS).

Results

We deployed 153 radio-transmitters (71 adult males, 21 yearling males, 2 juvenile males, 35 adult females, 22 yearling females, and 2 juvenile females). Seasonal survival estimates were obtained for 145 radio-marked sage-grouse (males n = 89, females n = 56). We recorded 64 radio-marked sage-grouse mortalities.

The average annual survival rate for all radio-marked sage-grouse during the study was 53% (95% CI = 49–56%; n = 195). The top ranking models included a combination of capture area and season survival (Table 1). Survival estimates for sage-grouse on the west and east side of BLPV were 90% (95% CI = 71–100%) and 50% (95% CI = 40–59%), respectively. Seasonal survival estimates for sage-grouse on the BLPV were: 1) spring 85% (95% CI = 79–89%); 2) summer 79% (95% CI = 71–86%); 3) fall 94% (95% CI = 87–98%); and 4) winter 83% (95% CI = n/a).

Annual survival rates for males and females were 50% (95% CI = 38–61%) and 57% (95% CI = 44–71%), respectively. Adult and yearling survival was 49% (95% CI = 39–59%; n = 102) and 67% (95% CI = 49–85%; n = 43), respectively. Annual survival was 52% (95% CI = 35–69%) in 2010, 66% (95% CI = 53–80%) in 2011, and 40% (95% CI = 26–54%) in 2012. Annual survival rates did not differ for migratory (75%; 95% CI = 61–89%, n = 38) and non-migratory radio-marked sage-grouse (73%; 95% CI = 60–86%, n = 51).

Nest success and brood survival

In 2011, 11 of 24 radio-marked hens initiated nests (46%). Clutch size ranged from 3–6 eggs with an average of 5 eggs. In 2012, 17 of 28 radio-marked hens initiated nests (61%). Clutch size ranged from 4–7 eggs, with an average of 6 eggs. The top AICc model for predicting nest success with uninformative parameters removed was the null model (Table 2). Two models ranked higher than the null model: VOR measurement and distance to the nearest tall anthropomorphic structures. Because these models had a great deal of uncertainty (ΔAICc < 2), we used the null model for analysis.

The daily nest survival rate using the null model was 96% (SE = 1%). The probability of any nest surviving from initiation to hatching was 22% (95% CI = 7–38%). The mean probability of nest success varied annually, with lower success rates recorded in 2011 (10%; 95% CI = 0–26%) than 2012 (31%; 95% CI = 9–54%). Overall, adult nest survival was higher (26%; 95% CI = 7–44%) than for yearlings (10%; 95% CI = 0–32%). The high variability observed between year and age could be attributed to low sample sizes.

In 2011, we documented 3 broods. Of these, 1 brood failed within a week of hatching and 1 brood failed within 3 weeks of hatching. The third brood was recorded for 14 days with at least 3 chicks still alive, but the hen's radio-transmitters failed shortly after that. In 2012, we documented 7 broods, and 1 brood failed 3 weeks after hatching. The other broods had at ≥1 chick survive to 50 days (86% brood success rate).

Nest and brood site selection

Models of VOR measurement and distance to the nearest anthropogenic structure for nest success ranked higher than the null model, but were not significant (Table 2). Vegetation variables including VOR, nest shrub diameter, and total grass percent and height differed between nest and random sites ($P < 0.05$; Table 3). Slope was the only micro-site variable that differed between brood and random sites ($P < 0.05$; Table 4).

Seasonal movements

We obtained location data for 153 radio-marked sage-grouse (males, n = 94; females, n = 59). However, radio-transmitter failure (n = 2) and inadequate sampling (n = 28) resulted in a sample size of 123 (males, n = 74; females, n = 49). For these radio-marked birds, we used individual shapefile to assess migratory seasonal movements. Twenty-eight percent (n = 43) of the marked individuals moved <10 km seasonally, 24% (n = 36) of marked individuals moved ≥10 km seasonally, and we could not determine migratory status for 48% (n = 74) of individuals because the annual relocation data were insufficient. Of the 36 individuals that moved ≥10 km to distinct seasonal ranges, we classified 97% as one-stage migratory (n = 35; 16 females and 19 males), and 3% as two-stage migratory (Connelly et al. 2011*a*). Migration timing and seasonal habitat use duration varied by year and individual bird. The average distance between each seasonal range was 25 km (SE = 5 km).

For females, the average Euclidean distance from a nest site to the nearest lek was 2.7 km (SE = 0.9 km), ranging from 0.2–11.4 km. Average Euclidean distance from the lek of capture to nest site was 3.5 km (SE = 1.3 km) with distances ranging from 0.5–13.4 km. The average Euclidean distance for broods from nest location was 747 m (SE = 283 m) from 0–14 days, 1,528 m (SE = 557 m) from 15–28 days, and 2,082 m (SE = 624 m) from 29–60 days.

Home range

The MCP and LoCoH home ranges were also generated to allow comparison of BLPV sage-grouse home ranges to other studies (see Cardinal 2015). Average annual KDE home range area was 101 km^2 (SE = 15 km^2). Average annual male and female KDE home ranges differed ($P < 0.01$). The average female annual KDE home range area was 59.4 km^2 (SE = 12.5 km^2), and the average annual male KDE home range area was 131.8 km^2 (SE = 24.5 km^2). Average KDE home ranges also differed for adult and yearlings ($P = 0.05$). The average annual yearling KDE home range area was 138.5 km^2 (SE = 43.3 km^2), and the average annual adult KDE home range area was 85.7 km^2 (SE = 12.6 km^2).

Discussion

The annual survival rates we recorded for BLPV sage-grouse were within range-wide estimates (30–78%; Connelly et al. 2011*a*). Female survival estimates were slightly higher than male estimates, and yearling survival was slightly higher than adult, which has been reported in other sage-grouse studies (Bunnell

Table 2. Models assessing the impact of temporal and habitat factors on nest survival of greater sage-grouse (*Centrocercus urophasianus*), Bear Lake Plateau and Valley study area, Idaho-Utah, USA, 2011–2012.

Model	K[a]	AICc[b]	Δ AICc[c]	*w*[d]
Robel in	2	130.42	0.00	0.12
Distance to structure	2	130.86	0.43	0.09
Null	1	131.42	0.99	0.07
Year	2	131.44	1.01	0.07
Litter percentage	2	131.64	1.22	0.06
Aspect	2	131.98	1.56	0.05
Distance to fence	2	132.42	2.00	0.04
Hen age	2	132.60	2.17	0.04
Total shrub height	2	132.93	2.17	0.03
Nest shrub diameter	2	133.01	2.58	0.03
Forb percentage	2	133.01	2.59	0.03
Grass percentage	2	133.05	2.62	0.03
Rock percentage	2	133.05	2.62	0.03
Forb height	2	133.05	2.63	0.03
Distance to lek	2	133.14	2.71	0.03
Total shrub height	2	133.29	2.86	0.03
Nest shrub height	2	133.39	2.97	0.03
Distance to road	2	133.42	2.99	0.03
Slope	2	133.42	2.99	0.03
Bare percentage	2	133.42	3.00	0.03
Artemisia spp. percentage	2	133.43	3.00	0.03
Shrub percentage	2	133.43	3.01	0.03
Grass height	2	133.43	3.01	0.03
Capture area	4	133.71	3.29	0.02

[a] K: number of parameters in each model
[b] AICc: Akaike Information Criterion corrected for small sample size
[c] Δ AICc: difference between a model and the best performing model
[d] *w*: Akaike model weight

2000, Zablan et al. 2003, Dahlgren 2006). Our top models for predicting survival included a combination of capture area and seasonal variation.

Cardinal (2015) analyzed factors affecting sage-grouse habitat selection in the BLPV. She reported the western side of Bear Lake exhibited greater habitat fragmentation and smaller habitat patch sizes. Beck et al. (2006) previously reported higher mortality for juvenile sage-grouse in fragmented landscapes because sage-grouse moved greater distances to meet seasonal habitat requirements. In our study, the average seasonal Euclidean distance radio-marked sage-grouse moved from capture leks on the west side of the Bear Lake was less than for sage-grouse captured on leks located east of the lake (Cardinal 2015). Habitat requirements may be met in a smaller area on the western side of the study site, which would reduce the distances sage-grouse need to travel to meet their seasonal needs.

Other studies have reported seasonal effects on survival (Connelly et al. 2000*b*, Wik 2002). The radio-marked sage-grouse in our study area were the most vulnerable during breeding season. Our sage-grouse survival estimates were the lowest in summer, when males are lekking and females nesting. Also, overwinter survival on the BLPV was on the low end of range-wide estimates. The BLPV is a high-elevation area that often experiences heavy snowfall, deep snow pack, and harsh temperatures. Poor winter habitat and lack of low-elevation winter refuges may negatively affect winter sage-grouse survival during severe weather (Moynahan et al. 2006, Anthony and Willis 2009, Connelly et al. 2011*a*, Caudill et al. 2013, Dahlgren et al. 2015*a*). Dahlgren et al. (2015*a*) reported high over-winter mortality in 2010 and 2011 for sage-grouse populations that used winter ranges within this basin where sagebrush removal treatments had been completed over a 24-year period.

Sage-grouse nest success is an important factor in sage-grouse population dynamics (Taylor et al. 2012, Dahlgren et al. 2016*b*). Range-wide nest success rates reported in other studies varied from 15–86% (Trueblood 1954, Gregg 1991, Schroeder et al. 1999, Connelly et al. 2011*a*). Both apparent hen nest success (27% in 2011 and 41% in 2012) and calculated nest success in the BLPV (10% in 2011 and 31% in 2012) were at the lower range of rates for sage-

Table 3. Vegetation characteristics at greater sage-grouse (*Centrocercus urophasianus*) nest sites compared to random sites in the Bear Lake Plateau and Valley study area, 2011–2012.

	Nest (n = 26)		Random (n = 21)	
	$\bar{x}$	SE	$\bar{x}$	SE
Aspect	164.5	32.0	159.0	43.7
Slope	9.4	3.4	9.7	3.6
Cover %				
Shrub	28.6	5.9	21.7	6.9
Artemisia spp.	25.4	5.2	15.7	4.8
Forb	17.5	4.1	12.1	3.6
Grass	14.1	2.5	18.9	2.8
Bare ground	20.4	5.3	15.1	3.5
Litter	30.4	4.9	35.0	6.1
Rock	8.3	4.3	8.2	3.9
Cover height (cm)				
Shrub	37.2	6.3	33.9	6.3
Artemisia spp.	40.1	7.4	35.5	6.1
Forb	7.0	1.1	6.5	1.1
Grass	16.3	1.9	20.0	3.1
Nest shrub				
Height (cm)	64.2	10.6	49.8	12.7
Diameter (cm)	118.9	20.4	66.4	14.7
Robel in (dm)	43.7	7.6	23.5	8.7

Table 4. Vegetation characteristics at greater sage-grouse (*Centrocercus urophasianus*) brood sites compared to random sites in the Bear Lake Plateau and Valley study area, 2011–2012.

	Brood (n = 24)		Random (n = 9)*	
	$\bar{x}$	SE	$\bar{x}$	SE
Aspect	154.5	46.5	154.5	46.5
Slope	3.8	1.4	3.8	1.4
VOR (dm)	27.5	7.3	27.5	7.3
Cover %				
Shrub	23.3	6.4	23.3	6.4
Artemisia spp.	21.0	5.9	21.0	5.9
Forb	11.3	2.7	11.3	2.7
Grass	16.9	3.0	16.9	3.0
Bare ground	15.2	3.5	15.2	3.5
Litter	38.9	4.8	38.9	4.8
Rock	5.5	3.6	5.5	3.6
Cover height (cm)				
Shrub	37.2	9.7	37.2	9.7
Artemisia spp.	35.9	9.6	35.9	9.6
Forb	9.0	2.9	9.0	2.9
Grass	21.9	3.8	21.9	3.8

* In the pilot year, unmarked broods were observed and vegetation was recorded, but because of constraints, not all random matched locations were measured.

grouse populations.

The BLPV clutch sizes were lower than sage-grouse clutch sizes reported from studies throughout their range (Connelly et al. 2011*a*). These lower clutch sizes may have resulted from eggs having been removed by predators before nest investigation, or from inclusion of re-nesting attempts, as clutch sizes in first nest attempts tend to average 2 eggs greater than a second nest attempt (Kaczor 2008). During trapping, we captured 2 females that had brood patches. These females subsequently initiated nests, providing evidence that sage-grouse in the BLPV may re-nest under suitable conditions after an early nest failure (Connelly et al. 1993, Kaczor 2008).

Nest distance to nearest lek ranged widely from 0.2–11.4 km. Previous research shows that female sage-grouse in anthropogenic fragmented habitats moved farther from leks to nest sites compared to birds occupying contiguous habitats (Wakkinen et al. 1992*a*, Schroeder 1997, Schroeder et al. 1999). However, Dahlgren et al. (2016*a*) reported the opposite for female sage-grouse radio-marked in Utah during the breeding season. Their radio-marked birds inhabited areas that exhibited increased natural fragmentation related to vegetation composition and topography. The authors attributed reduced female sage-grouse movements during the breeding season to limited habitat availability and space. Cardinal (2015) attributed the habitat fragmentation in the BLPV landscape to increasing anthropogenic development.

Vegetation composition has been reported to be a factor in nest selection and success Connelly et al. 2011*b*). The radio-marked females we monitored preferred big sagebrush for nesting, but other shrubs and grass were also used (Connelly et al. 1991, Dahlgren 2006, Connelly et al. 2011*b*, Robinson and Messmer 2013). Nesting females selected shrubs exhibiting larger canopies for nesting than recorded at random sites, which is consistent with range-wide observations (Sveum et al. 1998, Knerr 2007, Connelly et al. 2011*b*). Similar to studies range-wide, the sagebrush canopy around nest sites on the BLPV averaged 25% (Wallestad and Pyrah 1974, Connelly et al. 2000*b*, Connelly et al. 2011*b*, Robinson and Messmer 2013). Females also selected areas with higher nest bowl VOR than random sites, which has also been reported by other studies (Herman-Brunson 2007, Kaczor 2008, Connelly et al. 2011*b*). Increased vegetation cover may provide greater concealment and contribute to reduced predation (Coates and Delehanty 2010, Hagen 2011, Doherty et al. 2014).

Range-wide studies have found predator avoidance is an important component for avian nest site selection and can affect nest success (Cresswell 2008). Sage-grouse may select nest sites to avoid avian predators (Conover et al. 2010, Dinkins et al. 2012). Successful sage-grouse nests in the BLPV were located farther from tall anthropomorphic structures. Sage-grouse may avoid anthropomorphic structures as an indirect means of avoiding avian predators, which may use these structures as perches (Messmer et al. 2013, Coates et al. 2014).

Temporal and spatial factors did not rank in our top models for predicting nest success. However, our nest survival model weights suggested some uncertainty in the variables we tested. With larger sample sizes, these factors we tested may have ranked higher in model selection. Factors such as inter-annual variation, climate, hen age, and capture area have been found to influence nest success in studies with larger samples sizes, which can reduce variation associated with estimates (Connelly et al. 2011*a*).

Climatic variables have been found to influence nest success in sage-grouse (Caudill et al. 2014). The mean probability of nest success differed between 2011 and 2012 and may have been influenced by climate. Caudill et al. (2014) suggested winter snowfall, spring precipitation, and spring temperature could also affect nest survival. However, when we added annual precipitation to our nest survival models, it did not rank among our top models. With a larger nest sample size, the climatic factors may have surfaced as a factor influencing BLPV sage-grouse reproduction.

Brood success was also lower in 2011. Chick survival may be influenced by precipitation, temperature, and drought (Blomberg et al. 2012, Guttery et al. 2013). Wet conditions in 2011 may decreased brood success because chicks were more vulnerable to exposure mortality (Guttery et al. 2013). In 2012, from April to June, the temperatures were 5° warmer and the BLPV received half of the 2011 precipitation (Western Regional Climate Center 2013). Guttery et al. (2013) speculated that increased rainfall may increase predation rates on sage-grouse chicks, as mammalian predators may be more efficient in locating broods in wet conditions. Increased late-summer precipitation in 2012 could have increased forb and invertebrate production for chicks and brood production (Blomberg et al. 2012).

The forbs recorded at BLPV brood sites were common in other southern Idaho and northern Utah studies (Klebenow 1969, Graham 2013, Robinson and Messmer 2013). Forb composition was greater at nest sites than random sites, suggesting that females nested near areas that may have afforded increased forb availability during early brood-rearing. Gibson et al. (2016) reported similar observations in a 10-year study in Nevada.

Forbs are important in early and late brood-rearing areas as a food source for females and chicks (Dahlgren et al. 2015*b*). Forb cover at brood sites ranged from 0–24%, with an average of 11%. Connelly et al. (2000*b*) recommended >15 % forb cover as optimal for brood-rearing. However, total herbaceous cover (grass and forbs) was higher at brood than random sites, which has also been reported range-wide (Hagen et al. 2007). Sagebrush cover at brood sites was within habitat management guidelines suggestions (10–25%; Connelly et al. 2000*b*), with less sagebrush cover at brood sites than nest and random sites (Hagen et al. 2007).

Sage-grouse have previously been documented to travel large distances between seasonal ranges or as dispersal in yearling individuals (Connelly et al. 1988, Bradbury et al. 1989, Schroeder and Robb 2003, Reinhart et al. 2013). Some sage-grouse have been known to migrate over 161 km (Patterson 1952, Smith 2013). Individual BLPV radio-marked sage-grouse also engaged in extensive movements, which correlated with seasonal changes or with yearling dispersal (Cardinal 2015). Average distance between seasonal ranges on the BLPV was 25 km, which is greater than reported in previous literature, 11–30 km (Dunn and Braun 1986, Connelly et al. 1988). Though some individuals were migratory, most of the radio-marked sage-grouse we studied did not migrate.

The ability of individual sage-grouse to obtain resources on the landscape may influence migration patterns, as well as life stage, tradition, and landscape composition (Wallestad 1971, Fedy et al. 2012, Reinhart et al. 2013). The migratory radio-marked birds in our study had unique winter ranges. Fedy et al. (2012) reported similar findings in Wyoming. Like Fedy et al. (2012) and Dahlgren et al. (2016*a*), we documented high individual variability in BLPV sage-grouse migration patterns. Sage-grouse exhibited the greatest Euclidean average movement distances from the nearest lek during winter, suggesting that BLPV may lack sufficient winter cover and resources.

We located individual radio-marked sage-grouse well outside of the study area. Individual radio-marked sage-grouse annually moved as far north as Caribou County, Idaho, near the Bonneville County line and to the west in Bannock County, Idaho, which is a distance of 100 km. Long-distance movements have been observed in other studies (Patterson 1952, Connelly et al. 1988, Reinhart et al. 2013). The BLPV is located at the edge of the Wyoming Basin sage-grouse population (Stiver et al. 2006), and north and western movements were away from Wyoming Basin population centers. Thus, the BLPV sage-grouse population may provide an important genetic link between the Wyoming Basin and the Snake River Plain populations (Connelly et al. 2004).

Home ranges for sage-grouse can vary widely. Previous literature has reported annual home ranges from 4–615 km^2. Sage-grouse home ranges in the BLPV were within this range, with the average LoCoH home ranges of 12 km^2, MCP areas of 46 km^2, and KDE areas of 101 km^2. Variation in home range size may be explained by habitat requirements and resource needs (Connelly et al. 2011*a*). Female and male sage-grouse home ranges differed, with male annual home ranges almost twice the size of female home ranges. Male sage-grouse tend to make larger movements and cover more area than females (Connelly et al. 1988, Hagen 1999). The average home range size also differed for yearling and adult birds. Yearling sage-grouse are known to make large exploratory movements during dispersal (Dunn and Braun 1985), which could account for some of the variation we observed in home range sizes.

Different data collection techniques used to gather location information can yield large variations in home range size (Arthur and Schwartz 1999). Location and movement data collected using VHF data may not detect large individual movements because of the time constraints associated with collecting these data (Dahlgren et al. 2016*a*) and thus underestimate sage-grouse home ranges (Kochanny et al. 2009).

Different calculation techniques may also yield very different home range estimates (Lichti and Swihart 2011, Rudeen 2012). Sage-grouse home ranges have been estimated using minimum convex polygon, kernel density estimators, and local convex hull. Local convex hulls are a relatively recent technique for estimating home ranges (Getz and Wilmers 2004), which uses minimum convex polygons to create a convex hull around nearest neighbors. Larger sample sizes will increase the power of both KDE and LoCoH (Lichti and Swihart 2011). Because of our limited data, BLPV sage-grouse LoCoH estimates selected areas that were clustered and did not include movement corridors.

Management implications

Habitats in Bear Lake State Park and Bear Lake National Wildlife Refuge likely serve as movement corridors for dispersing and migrating sage-grouse. As such managers should place increased emphasis on protecting corridors linking core habitats from further development to provide viable genetic links between populations. Additionally, poor recruitment attributed to low nest, brood, and adult winter survival may be affecting sage-grouse population stability on the BLPV. However, we recommend caution when interpreting the results of this short-term study, because the variability we observed in nest and brood success may be reflective of environmental conditions and sample sizes. The overall contribution of nest and brood success to upland game population dynamics can only be determined by long-term research that is able to compare the relative effects of seasonal variation on vital rates (Dahlgren et al. 2016*b*). Because sage-grouse on the BLPV study area used seasonal habitats in Idaho, Utah, and Wyoming, increased cooperation among state agencies and local working groups in Idaho, Utah, and Wyoming could aid in landscape and population management efforts. The creation of a tri-state BLPV sage-grouse management plan assist in the conservation of important seasonal habitats found in all 3 states.

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