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Movements and Space-Use of Female Greater Sage-Grouse (*Centrocercus urophasianus*)

During Nesting and Breeding Seasons

Drew W Retherford

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

Movements and Space-Use of Female Greater Sage-Grouse (*Centrocercus urophasianus*) During Nesting and Breeding Seasons

Drew W Retherford
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Master of Science

Greater sage-grouse (*Centrocercus urophasianus*) are a species of conservation concern throughout their range including the state of Idaho. Little is known about the size of areas used by female sage-grouse during the breeding and nesting seasons, fidelity of females to those areas, or fidelity of female sage-grouse to specific leks or nest sites. The recent miniaturization of global positioning system (GPS) transmitting devices allows for a more thorough analysis of this behavior. We placed GPS transmitters on 234 female sage-grouse in Idaho, USA, from 2015 to 2019. We monitored 145 nest attempts, 15 of which occurred in consecutive years, from 130 female sage-grouse (*Centrocercus urophasianus*) with GPS transmitters to document movements and space-use during nesting. We quantified the length and direction of off-nest excursion distances for all 145 nest attempts. Also, for the 15 consecutive nest attempts, we compared the excursion distances for each bird, each year. The mean distance for an off-nest excursion across all study areas was 93.7 m ($n = 145$, $SD = 57.9$, range = 15.5 to 275.8 m). Rayleigh's test of uniformity indicated that eight of 145 nest attempts had off-nest excursions that were not in a consistent direction. Mean excursion distances in the consecutive year were longer than those of the initial year ($T = -3.1$, $n = 15$, p -value = 0.013), and females with smaller excursion distances in the initial year also had smaller excursion distances in the consecutive year. We also quantified size of breeding areas for 50 female sage-grouse and identified factors that influenced breeding-area size. For 18 of those females, we quantified size and fidelity to breeding areas and leks between successive years. We generated 95% brownian bridge estimates of breeding-area size for each bird and counted the number of leks those females visited. To quantify breeding-area fidelity for the 18 females, we overlaid 95% brownian bridge estimates for females with consecutive breeding attempts, calculated percent overlap, and documented number of leks visited each year. Median size of breeding areas for all females was 21 km² (interquartile range = 7.8 to 59.3 km²). Each bird visited a mean of 2 leks ($SD = 1.2$, range = 1 to 6 leks). Between years, breeding areas overlapped for all 18 females, and size of breeding areas did not differ between the first and second year (W -value = 61, p -value = 0.49). For those 18 females, only 7 visited the same lek in consecutive years, and none visited more than one common lek in consecutive years. Our results indicate that females use large areas while breeding and nesting and exhibit strong fidelity to those areas. Our results provide novel information on the breeding and nesting ecology of this species that will help agencies that manage sage-grouse and their habitat.

Keywords: sage-grouse, nesting, habitat, nest fidelity, lek, habitat, breeding movements

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CHAPTER 1

Movements and Space-Use of Female Greater Sage-Grouse (*Centrocercus urophasianus*) During Nesting

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ABSTRACT

Fidelity to breeding areas in birds is a common behavior, however, variation in fidelity exists within and across species and taxa. While fidelity to breeding areas is commonly studied in marsh and riparian habitats, less is known about breeding-area fidelity in upland game birds, such as sagebrush (*Artemisia* spp.) obligate species. The recent miniaturization of global positioning system (GPS) transmitting devices allows for a more thorough analysis of this behavior. We monitored 145 nest attempts, 15 of which occurred in consecutive years, from 130 female sage-grouse (*Centrocercus urophasianus*) with GPS transmitters to document movements and space-use during nesting in Idaho, USA, from 2015 to 2019. We quantified the length and direction of off-nest excursion distances for all 145 nest attempts. Also, for the 15 consecutive nest attempts, we compared the excursion distances for each bird, each year. The mean distance for an off-nest excursion across all study areas was 93.7 m ($n = 145$, $SD = 57.9$, range = 15.5 to 275.8 m). Rayleigh's test of uniformity indicated that eight of 145 nest attempts had off-nest excursions that were not in a consistent direction. Mean excursion distances in the consecutive year were longer than those of the initial year ($T = -3.1$, $n = 15$, p -value = 0.013), and females with smaller excursion distances in the initial year also had smaller excursion distances in the consecutive year. Our results indicate that nesting female sage-grouse use small areas while

nesting and further emphasize the importance of managing sage-brush steppe ecosystems so as to be suitable for nesting sage-grouse.

INTRODUCTION

Fidelity to breeding areas in birds is a common behavior, however, variation in fidelity exists within and across species and taxa. For example, 88% of adult male and female great reed warblers (*Acrocephalus arundinaceus*) showed a high degree of fidelity to the original breeding habitat in which they were banded (Mero et al. 2018). Also, both sexes of little ringed plovers (*Charadrius dubius*) exhibited high (72-99%) fidelity to breeding sites between years (Pakanen et al. 2015). Avian species may demonstrate fidelity to breeding areas due to resource availability (Borrmann et al. 2019; Wiebe 2018) and higher fledging rates because of parental familiarity with the area (Beletsky and Orians 1991; Yezerinac et al. 2013). There may also be negative consequences to breeding area fidelity, such as increased rates of inbreeding (Nemeshazi et al. 2018; Saunders et al. 2018; Soulsbury et al. 2012) or predators keying in on consistent prey sources (Benvenuti et al. 2018; Wang et al. 2018), which may deter such behavior. Most research has focused on breeding-area fidelity in passerines (Mero et al. 2018; Pakanen et al. 2015), however, comparably little work has been done on fidelity to breeding areas in other taxa.

While fidelity to breeding areas is commonly studied in marsh and riparian habitats, less is known about breeding-area fidelity in upland environments, such as sagebrush-steppe (*Artemisia* spp.). Greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) are an upland species reliant on sagebrush ecosystems in all phases of their life cycle. This species follows a polygynous breeding system and both males and females congregate on communal

breeding grounds (called leks) each spring (Bradbury et al. 1989; Wiley 1978). Males of this species exhibit a 97% rate of fidelity across years to the lek on which they were captured (Gibson et al. 2014). Probability of daily movement between leks by males is extremely low, estimated at between 0.3 and 1.0% (Fremgen et al. 2017). Very little information exists, however, concerning breeding-area fidelity of females. Understanding fidelity to breeding areas can be critical for the conservation of upland species and their habitats, especially for sage-grouse as low recruitment has been implicated as a cause of population declines (Beck et al. 2003; Swenson et al. 1987; Taylor et al. 2018).

A critical component of breeding-area fidelity in birds is nest-site fidelity. Nest-site fidelity is likely driven by several factors, however, exact causes are difficult to identify (Herzog et al. 2018). Fidelity to nest sites and natal areas may increase inclusive fitness through brood parasitism and merging of family groups from related individuals in new world waterfowl (*Anatidae* spp.) and quail (*Odontophoridae* spp.) (Andersson 2018). Individual reproductive success could be the major factor in determining breeding dispersal in collard flycatchers (*Ficedula albicollis*) (Doligez et al. 1999). Moreover, habitat-use based on resource availability is a well-documented behavior (Coron et al. 2018; Evens et al. 2018; Oguchi et al. 2018) and may contribute to nest-site fidelity. Nonetheless, for two populations of sage-grouse, success of nesting females had no effect on the distances between nest-sites in consecutive years (Fischer et al. 1993; Peck et al. 2012).

The recent miniaturization of global positioning system (GPS) transmitting devices allows for a more thorough analysis of female sage-grouse movements and habitat use during nesting (i.e. multiple accurate locations per day with consistent intervals). Although there are drawbacks and limitations to GPS transmitting devices such as accuracy, weight, and cost

(Bouten et al. 2013), the use of GPS collars is generally considered superior to very high frequency (VHF) transmitters (Tomkiewicz et al. 2010). Nest-site fidelity in female sage-grouse using triangulation from VHF transmitters is documented (Fischer et al. 1993; Peck et al. 2012). However, with GPS transmitting devices it becomes possible to document sufficient relocations to do in-depth spatial analysis (Tomkiewicz et al. 2010). Such spatial analysis can provide greater insight into fidelity to nesting areas and resource needs of females during this important part of the life cycle.

Space use by nesting female sage-grouse is an important aspect of their annual ecology as low nest success has been identified as contributing to population declines for this species (Aldridge and Brigham 2001; Connelly and Braun 1997). We monitored 130 female sage-grouse with GPS transmitters to document movements and space-use during nesting in southern Idaho, USA, from 2015 to 2019. We hypothesized that female sage-grouse would use similar areas when nesting each year and have similar movement patterns (i.e., distance and direction) while nesting. We predicted that females would nest in designated priority habitat that was implemented for Idaho sage-grouse conservation (Otter 2012), and that the nest excursion distances of females would be influenced by study area and habitat designation (Otter 2012). We also predicted female sage-grouse would move in random directions during off-nest excursions. Additionally, we predicted that the distances between nest sites in consecutive years would be within 1,000 m as documented in other studies (Fischer et al. 1993; Peck et al. 2012), and that the mean distance of nesting excursions for those females would be similar across years. Our results will provide information on the size of area that female sage-grouse need to nest and how female sage-grouse disperse through nesting habitat across years, which will help identify sage-grouse nesting habitat for future conservation and management actions.

STUDY AREA

We captured female sage-grouse in four populations in southern Idaho (Fig. 1.1) including the Big Desert, Greater Curlew Valley, areas surrounding Salmon, Idaho, and the Sand Creek Desert. Each study area consisted of sagebrush-steppe habitat, which was made up of a juxtaposition of dry land brush communities with more open areas occurring in mesic sites and disturbed areas (Leonard et al. 2000). Mixed/mountain shrub habitat types occurred within moist drainages and on north aspects. Topography in our study areas consisted mostly of low rolling hills in the valley bottoms moving into higher elevation ranges on the periphery of suitable sage-grouse habitat. Livestock grazing on both private and public land occurred in all four study areas. Sharp-tailed grouse (*Tympanuchus phasianellus*) were also present in each of these study areas. Additionally, several species of predators occurred in our study areas that have been documented to prey on sage-grouse and their eggs. Those predators included red fox (*Vulpes vulpes*), badger (*Taxidea taxus*), coyote (*Canis latrans*), and avian predators, such as golden eagle (*Aquila chrysaetos*) and common raven (*Corvus corax*) (Coates et al. 2008; Kammerle and Storch 2019; Kirol et al. 2018).

The Big Desert (43.266156, -113.152755) is located approximately 35 miles west of Blackfoot, Idaho. The big desert consisted almost entirely of federal lands managed by the BLM, however, there was limited amounts of both private land and lands managed by the State of Idaho. Irrigated agricultural fields were present on both the southern and eastern borders along the Snake River. Native plant communities were mostly sagebrush steppe consisting primarily of mountain big sage (*A. t. vaseyana*) at lower elevations with mixed/mountain shrub communities at higher elevations.

The Greater Curlew Valley (42.184135, -112.647527) was a sagebrush-dominated valley with foothills bisecting the Idaho and Utah borders (Fischer et al. 1993). Public lands were managed by the US Bureau of Land Management (BLM) and the United States Forest Service (USFS), although large amounts of the valley bottom were privately owned. Conservation of sagebrush communities was a priority for land management agencies in that area, with goals of preserving areas of intact sagebrush. Native plant communities were primarily Wyoming big sagebrush (*A. t. wyomingensis*) in the valley bottoms and mixed mountain shrub communities at higher elevations with pinyon (*Pinus monophylla*)-juniper (*Juniperus* spp.) woodlands spread throughout.

The area surrounding Salmon, Idaho (45.174782, -113.896917) consists of both the Big Lost and Little Lost valleys, which are separated by the Lemhi Mountains. The valley bottoms were farmed for various irrigated and dry-land crops. However, from the valley bottoms to the coniferous tree lines was abundant mountain big sagebrush communities which provided habitat for sage-grouse (Yeo 2005).

The Sand Creek Desert (44.198243, -111.918194) is located in the Upper Snake River Plain. The Sand Creek Desert consisted of a combination of private and publicly-owned land. Public lands were managed by the BLM and the state of Idaho. Irrigated agricultural fields were common along the southern border.

The Idaho Department of Fish and Game, BLM, USFS, and U.S. Fish and Wildlife Service classified sage-grouse habitat in the state of Idaho into three designations: priority habitat management areas (PHMA), important habitat management areas (IHMA), and general habitat management areas (GHMA) for sage-grouse conservation (Otter 2012). PHMA and IHMA contained over 90% of the leks and 95% of displaying male sage-grouse located in the

state of Idaho (Otter 2012). Designation of PHMA and IHMA habitat was designed to preserve two metapopulations consisting of smaller breeding subpopulations (Otter 2012). Portions of our study areas included habitats from all three designations. Approximate proportions of each designation for all study areas lumped together were 32% PHMA, 28% IHMA, 13% GHMA, and 27% not part of any of these habitat designations.

METHODS

Capture, Collaring, and Tracking

During spring 2015-2019, we captured female sage-grouse using rocket nets and spotlighting methods (Wakkinen et al. 1992). Captures were conducted by personnel from the BLM, USFS, and Idaho Department of Fish and Game. Sex of the bird was determined at capture by observing the coloration of primary flight feathers (Braun and Schroeder 2015). Age class (adult or juvenile) of sage-grouse was also determined at capture by observing molting feathers of the wing and the shape of the primary feathers (Braun and Schroeder 2015). Female sage-grouse were fitted with GPS Platform Transmitter Terminal (PTT) rump-mounted transmitters (22-gram Solar Argos/GPS PTT-100, Microwave Telemetry Inc.). PTT transmitters were programmed to transmit six points a day in spring/summer and 3 points a day during fall/winter.

After downloading GPS transmitter data, we removed locations with a dilution of precision value > 10 to ensure accuracy of locations (D'Eon and Delparte 2005; Lendrum et al. 2013). To quantify accuracy of PTT transmitters, we placed a transmitter in sage-grouse nesting habitat for 28 days. That transmitter location was then recorded using a high-accuracy GPS unit (Trimble GEO XH 6000, Trimble Inc., Sunnyvale, California). PTT transmitter accuracy was

verified at ± 14.3 m. Transmitters were also equipped with an ultra-high frequency (UHF) transmitter, which we used to locate grouse or PTTs at close range.

We estimated nest locations by observing when GPS coordinates were recorded from the same location for > 5 days without movements > 150 m indicating that the female had begun incubation. To locate nest bowls, we traveled within UHF range of the estimated location and used hand-held UHF receivers (DJ-X11, Alinco inc., Osaka Japan), 3-element Yagi antennas, and binoculars to locate nesting females without flushing them. Termination of the nesting attempt was determined when GPS data showed that the female had moved away from the nest area by > 300 m for > 2 days. Using GPS data, we determined nest abandonment if GPS coordinates were documented moving away from the nest location before the expected hatch date by > 300 m for > 2 days. We estimated hatch dates to be 26-28 days from initiation of incubation (Coates and Delehanty 2008). We visited nest locations after hatching or abandonment to confirm nest fate based on egg shell fragments (Whitehead and Turner 1998).

Data Analysis

We imported nest locations into ArcGIS® (ESRI, Redlands, California USA) and recorded the habitat designation in which they were located. To determine average distance of off-nest excursions, we used the pointDistance function in the raster package (Hijmans and Van Etten 2012) in R (R development team 2008) as this method did not overestimate areas used by nesting females. We calculated a mean distance from all points to the nest site to determine average length of off-nest excursions. Points within 15 m of the nest sites were excluded to account for GPS fix error as grouse may not have been off-nest. To test for differences in proportions of nests per habitat designation, we performed a G-test of proportions. In order to

determine the degree of directionality in off-nest locations, we used the *circstats* (Lund and Agostinelli 2001) package to calculate Rayleigh's test of uniformity and used a Bonferroni-corrected α value to determine significance of each test (Shi et al. 2012).

To compare possible factors influencing average off-nest excursion distances, we used a mixed-effects linear regression model from the *lme4* package (Bates et al. 2015). Our fixed-effects explanatory variables were age, study area, previous year's success, and habitat classification. Random effects were the calendar year in which the nest attempt occurred (year) and the number of years that we had documented nesting attempts for that female (nesting year) (Table 1.1). We checked variables prior to model construction for correlation using the *cor* function in R to verify no values were greater than |0.6|. To evaluate relative model support, we judged models based on minimization of Akaike's Information Criterion adjusted for small sample sizes (AICc) and the final model table was screened for uninformative parameters (Akaike 1973; Anderson and Burnham 2002; Arnold 2010; Wagenmakers 2003). To ensure significant sample sizes for statistical analysis, we combined GHMA and IHMA habitat designations into a single category. Any females that nested outside of any designation were classified as NONE for our statistical analysis. We also performed a paired t-test to determine if there was a significant difference in off-nest excursion distances between the initial and consecutive nests for females with consecutive years of nesting data. We produced a correlation plot to represent the difference between the initial and consecutive-year off-nest excursion distances. To produce our correlation plot of consecutive year off-nest excursion distances, we removed outlying data by excluding five individuals that were greater than two standard deviations from the mean.

RESULTS

We captured 234 female greater-sage-grouse on and around leks during spring. One hundred and four female sage-grouse were excluded from use in our study due to mortality or loss of transmitter during the first year before sufficient data had been collected. Female sage-grouse in our study areas initiated nests between April 12 and June 20, 2015 to 2019. During this period, we collected 6,186 locations during nesting for 130 female sage-grouse (mean = 34 relocations per grouse, SD = 28.1 relocations) across 145 discrete nesting attempts in our analysis. Of 145 discrete breeding attempts, 21 were located in the Big Desert, 22 were located in the Greater Curlew Valley, 19 were located in the Salmon area, and 83 were located in the Sand Creek Desert. Of these 145 nesting attempts, 71% nested in PHMA, 18% nested in IHMA, and 3% nested in GHMA, with 8% nesting outside any designation (classified as NONE). A significant difference existed in the proportions of nests found within each habitat designation (G -value = 73.0, p -value = 0.03).

The global model was the top-ranked model in our analysis of off-nest excursion distances (Table 1.2). Our top-ranked model contained 0.90 of the AICc weight (Table 1.2). Habitat designation and year were the only variables that were included in all models that carried any weight (Table 1.2). Success was the only variable in our top model that did not contain zero within the 85 percent confidence interval around the beta estimate, but several other variables were close to excluding zero from the intervals (Table 1.3). The mean distance for an off-nest excursion in all study areas was 93.7 m ($n = 145$, SD = 57.9, range = 15.5 to 275.8 m). Excursion distances by study area were 88.3 m ($n = 21$, SD = 37.7) for the Big Desert, 65.3 m ($n = 22$, SD = 40.8) for Greater Curlew Valley, 91.8 m ($n = 19$, SD = 71.8) for the Salmon study area, and 101.1 m ($n = 83$, SD = 59.7) for Sand Creek Desert. There was no difference in excursion

distance by habitat designation. Rayleigh's test of uniformity indicated that only eight of 145 nest attempts did not leave in a consistent direction (Fig. 1.2). Of 15 females for which we had consecutive years of nesting data, 2 were located in the Big Desert, 3 were located in the Greater Curlew Valley, one was located in the Salmon area, and 9 were located in the Sand Creek Desert. Of those, 12 nested in PHMA, two nested in IHMA, and one nested in GHMA. The median distance between consecutive nests was 436.7 m ($n = 15$, $SD = 1351.3$ m). The mean excursion distance in the consecutive year were longer than those of the initial year ($T = -3.1$, $n = 15$, p -value = 0.013, Fig. 1.3), and females with smaller excursion distances in the initial year also had smaller excursion distances in the consecutive year (Fig. 1.4).

DISCUSSION

We predicted that female sage-grouse would nest in priority habitat designated for Idaho sage-grouse conservation (Otter 2012). Our data indicated that there was a difference in the number of nests located within each habitat designation. There were more nests located in PHMA than any other habitat designation (PHMA = 103, all other designations = 42) supporting our prediction that more nests would be located in PHMA than other designations. This result was expected because historical nest location data was used by managing agencies to determine designation boundaries (Otter 2012). Lek locations were also used to assign designations and previous research has linked nesting habitat to lek proximity (Connelly et al. 2000). Also, PHMA designated areas are more restrictive for development and such restrictions should result in higher quality nesting habitat, which would promote higher recruitment in those areas (Aldridge and Boyce 2007; Dinkins et al. 2016). The nonrandom assignment of habitat designations introduced a level of bias as priority habitat designation was given to the areas that had the

largest population of nesting sage-grouse and other features that indicated large numbers of nesting sage-grouse (i.e. lek proximity, intact nesting habitat). However, we also documented that eight percent of nests were not included in any habitat designation and we recommend that managing agencies consider adjusting habitat designation boundaries to include these nesting areas. This result highlights the effectiveness of these designations and reinforces the value of the restrictions placed on these critical areas for sage-grouse conservation.

We also predicted that females would move in random directions during off-nest excursions. All but eight female sage-grouse ($n = 130$ unique individual grouse; 145 nesting attempts), however, left the nest in a uniform direction. These data are the first published assessment of this measure for sage-grouse, although other avian species displayed similar behavior (Marzluff and Neatherlin 2006; Sachot et al. 2003). In one study common ravens were documented leaving nest sites in certain directions toward resource areas (Marzluff and Neatherlin 2006). Our results are likely due to heterogeneity within sagebrush habitats and grouse moving to higher-quality resource patches. Research has been conducted to generally characterize sage-grouse nesting habitat (Connelly et al. 2000; Connelly et al. 1991). This information provides important insight into nesting ecology of female sage-grouse as nest success has been identified as a contributing factor to recent population declines (Aldridge and Brigham 2001; Connelly and Braun 1997).

We hypothesized that female sage-grouse would use similar areas when nesting in consecutive years and have similar movement patterns (i.e. distance and direction) while nesting across years. We documented a median distance between consecutive-year nests of 436.7 m. This result was similar to previous research from Utah (Peck et al. 2012) and Idaho (Fischer et al. 1993). This result also supports the conclusions of the previous research that female sage-

grouse return to similar areas to nest across years (Berry and Eng 1985; Schroeder and Robb 2003). Fidelity to nest areas provides females with familiar areas in which to nest and acquire resources (Gerber et al. 2019). Fidelity also heavily influences space use, seasonal movements, and gene flow (Gerber et al. 2019). Our results highlight the importance of preserving sage-grouse nesting habitat as grouse return to nest in similar areas each year and nest success has been identified as a factor in sage-grouse population declines (Aldridge and Brigham 2001; Connelly and Braun 1997). Also, previous research has indicated that nesting sage-grouse are unable to adapt to rapid changes in their habitat leading to a decrease in clutch size and population declines (Beck et al. 2003; Schroeder 1997; Swenson et al. 1987).

We predicted that length of off-nest excursions would be similar across years. Our paired t-test indicated that there was a correlation in the nest excursion distances between years with initial-year distances smaller than off-nest excursion distances observed in consecutive years. In previous research, weather has been a factor influencing breeding in sage-grouse (Bradbury et al. 1989; Fremgen et al. 2019). Our data, however, was collected over a span of five years with varying conditions and thus weather is unlikely to have caused the difference in excursion distances we observed in consecutive years. The presence of predators may also affect the behavior of breeding females (Boyko et al. 2004; Hartzler 1974) and may account for the differences between years. We hypothesize that this result is caused by females becoming more familiar with their nesting areas and venturing further to acquire necessary resources in the subsequent year (Aldridge and Boyce 2007; Sandford et al. 2017).

The time interval between successive fixes (programmed for 4 hours) on our GPS transmitters likely prevented us from capturing all off-nest excursions. However, with our large sample size we were able to collect enough data to perform analysis. Another potential limitation

was our lack of meaningful habitat data as small-scale habitat data may also influence the off-nest excursion distance and possibly the distances between nest sites in consecutive years. Future research should consider the effects that habitat factors have on the movements of nesting female sage-grouse.

Space-use by nesting female sage-grouse is an important aspect of their annual ecology as nest success rates have been identified as contributing to population declines (Aldridge and Brigham 2001; Connelly and Braun 1997). We documented that female sage-grouse returned to the same areas to nest in subsequent years and that more females nested in priority habitat (PHMA) than all other designations combined. Approximate proportions of each designation for all study areas lumped together were 32% PHMA, 28% IHMA, 13% GHMA, and 27% not part of any of these habitat designations. We also documented that female sage-grouse used relatively large areas while nesting, that the amount of area varied depending on age of the female, and that most female sage-grouse left the nest in a consistent direction. Additional insight into what specific resources female sage-grouse were using while off nests would provide valuable information to help identify and conserve nesting habitat. Our results further emphasize the importance of managing sage-brush steppe ecosystems so as to be suitable for nesting sage-grouse.

LITERATURE CITED

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FIGURES



Figure 1.1: Map of study area where we deployed platform transmitter terminal (PTT) units on female greater sage-grouse (*Centrocercus urophasianus*) to monitor movements and habitat use during nesting season in southern Idaho, USA, 2015-2019. The four greater sage-grouse populations included Big Desert, Greater Curlew Valley, Salmon, and Sand Creek Desert.

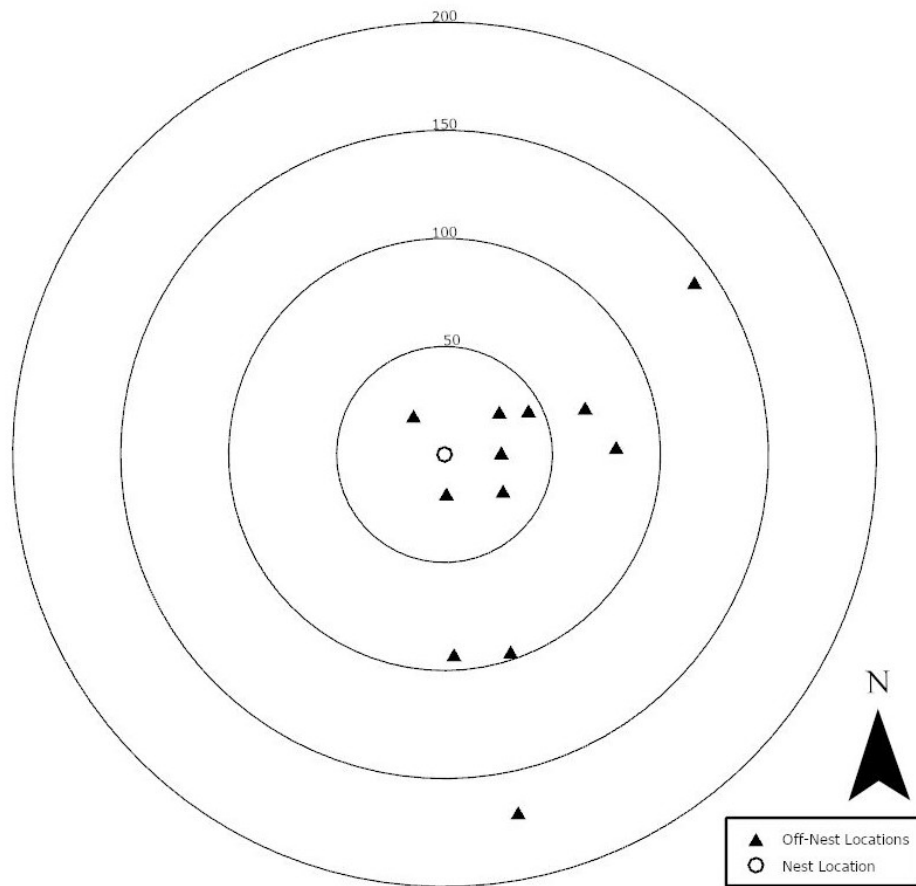


Figure 1.2: An example of off-nest excursions for a female greater sage-grouse (*Centrocercus urophasianus*) in a single nest attempt in southern Idaho, USA. Each concentric ring represents 50 m from the nest bowl.

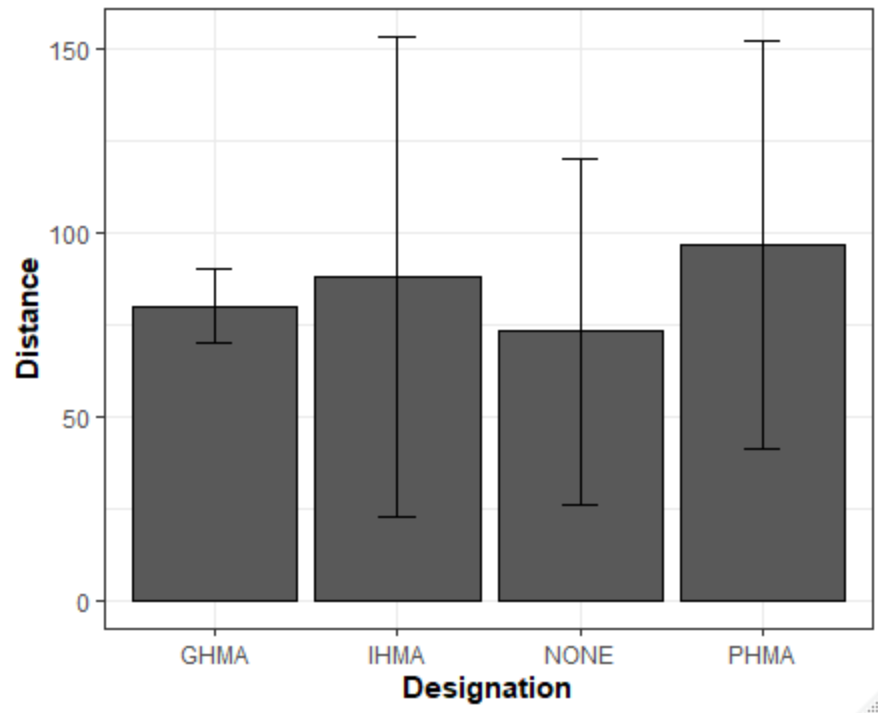


Figure 1.3: Average off-nest excursion distances for female greater sage-grouse (*Centrocercus urophasianus*) in each of our habitat designations from 2015 to 2019 in southern Idaho, USA.

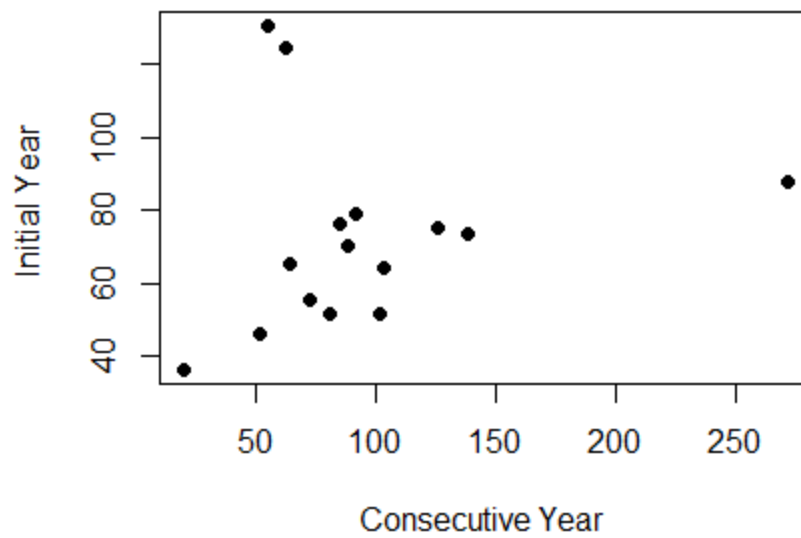


Figure 1.4: Correlation between initial and consecutive year excursion distances for 15 female greater sage-grouse (*Centrocercus urophasianus*) from 2015 to 2019 in southern Idaho, USA.

TABLES

Table 1.1: Name and description of each variable used to build models of the off-nest excursion distance by nesting female sage-grouse (*Centrocercus urophasianus*), southern Idaho, USA, 2015-2019.

Variable Name	Description
Excursion Distance	Average distance (in meters) of the off-nest excursion for a given nest attempt
Age	Age of female sage-grouse, given as Adult (A), Juvenile (J), or unknown (U)
Habitat Designation	The state of Idaho Habitat designation in which the nest was located
Nest Year	Year of observed nesting attempt by the female grouse
Success	Whether the female grouse successfully hatched ≥ 1 egg or failed the nest attempt
Year	Calendar year in which the nesting attempt occurred
Bird ID	ID number assigned to each bird
Study Area	The study area where the nest was located

Table 1.2: Model rankings (AICc and Δ AIC), model weights (w_i), number of estimated parameters (K), and log likelihood (LL) for supported models (model weight $\geq 1\%$) of off-nest excursion distances for 145 nesting attempts from 130 female sage-grouse (*Centrocercus urophasianus*), southern Idaho, USA, 2015-2019.

Model	Structure	AICc	Δ AIC	w_i	K	LL
nm1	Age + Habitat Designation + Nest Year + Success	1820.8	0.00	0.897	5	-898.53
nm16	Age + Habitat Designation + Nest Year	1826.4	5.60	0.055	4	-902.48
nm15	Habitat Designation + Nest Year + Success	1826.8	6.01	0.044	4	-902.67
nm12	Habitat Designation + Nest Year	1832.1	11.33	0.003	3	-906.48
nm14	Age + Habitat Designation + Success	1834.9	14.18	0.001	4	-907.90
nm9	Habitat Designation + Success	1840.3	19.58	0.000	3	-911.72
nm11	Age + Habitat Designation	1840.8	20.09	0.000	3	-911.97
nm6	Habitat Designation	1846.0	25.26	0.000	2	-915.66
nm13	Age + Nest Year + Success	1947.9	127.18	0.000	4	-964.44
nm10	Age + Nest Year	1953.1	132.36	0.000	3	-968.13
nm8	Nest Year + Success	1955.2	134.47	0.000	3	-969.19
nm5	Nest Year	1960.0	139.29	0.000	2	-972.70
nm7	Age + Success	1962.3	141.56	0	3	-973.83
nm4	Age	1967.7	146.90	0	2	-977.58
nm3	Success	1968.7	147.99	0	2	-978.13
nm2	Null Model	1973.8	153.03	0	0	-981.72

Table 1.3: Parameter estimates for variables included in our top model of off-nest excursion distances for 145 nesting attempts from 130 female sage-grouse (*Centrocercus urophasianus*). We report estimates, standard error (s.e.), lower (L85CI) and upper (U85CI) confidence intervals, Z-values and *p*-values.

Parameter	Estimate	s.e.	L85CI	U85CI	Z-value	<i>p</i> -value
Intercept	38.41	14.42	13.36	52.91	3.483	0.028
PHMA	10.37	4.211	-0.22	8.82	1.846	0.092
IHMA/GHMA	0.82	7.553	-4.26	5.33	2.126	0.587
NONE	-3.63	3.429	-8.13	0.42	0.658	0.862
Nest Year	-1.27	5.846	-2.47	6.23	1.013	0.745
Age	2.22	2.872	-2.04	11.38	0.624	0.552

CHAPTER 2

Space-Use of Female Greater Sage-Grouse (*Centrocercus urophasianus*) During the Breeding Season

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ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) are a species of conservation concern throughout their range including the state of Idaho. Little is known about the size of areas used by female sage-grouse during the breeding season, fidelity of females to those areas, or fidelity of female sage-grouse to specific leks where they gather each spring. We quantified size of breeding areas for 50 female sage-grouse and identified factors that influenced breeding-area size in Idaho, USA, from 2015 to 2019. For 18 of those females, we quantified size and fidelity to breeding areas and leks between successive years. We generated 95% brownian bridge estimates of breeding-area size for each bird and counted the number of leks those females visited. To quantify breeding-area fidelity for the 18 females, we overlaid 95% brownian bridge estimates for females with consecutive breeding attempts, calculated percent overlap, and documented number of leks visited each year. Median size of breeding areas for all females was 21 km² (interquartile range = 7.8 to 59.3 km²). Each bird visited a mean of 2 leks ($SD = 1.2$, range = 1 to 6 leks). Between years, breeding areas overlapped for all 18 females, and size of breeding areas did not differ between the first and second year (W -value = 61, p -value = 0.49). For those 18 females, only 7 visited the same lek in consecutive years, and none visited more than one common lek in consecutive years. Our results indicate that females use large breeding areas,

exhibit strong fidelity to those areas, but not to specific leks within those areas. Our results provide novel information on the breeding ecology of this species that will help agencies that manage sage-grouse and their habitat.

INTRODUCTION

Breeding strategies can vary greatly across taxa and even between individuals of the same species. In many species, sexual selection plays a key role in the strategies employed to attract mates (Darwin 1871). Breeding strategies serve a broad purpose in assuring that the most competitive mates are selected to ensure superior genetic inheritance and that offspring receive the best chance at survival (Ivy and Lacy 2012). In certain cases, differing breeding strategies will also assist in speciation and prevention of hybridization (Cunningham et al. 2018). Breeding strategies may consist of mating between multiple individuals (polygamy) (Emlen and Vehrencamp 1985) or mating between single individuals (monogamy) (Gray 1997; Kubo et al. 2018), although extra pair copulations may still be common for species with monogamous breeding strategies. Strategies to select competitive mates include tests of physical fitness (Clifton et al. 2015), defense of females (Simmons et al. 1986), or defense of home ranges (Gray 1997).

Use of leks (i.e. communal breeding areas) is a breeding strategy documented in various species from different taxa (Ciuti and Apollonio 2016; Silva et al. 2017; Toth and Parsons 2013). For species that practice this breeding strategy, males typically defend small areas on a lek where females visit to select a mate (Cross et al. 2017; Silva et al. 2017). Mating may occur on or off the lek (Bradbury et al. 1989). Lek breeding is typically found in scenarios where males cannot defend home territories containing enough resources or protect females from mating with

competing males (Shelly 2018). In these circumstances, this strategy offers increased breeding opportunities for dominant males and provides females with larger groupings of males from which to select a mate. Females can then breed with the most dominant male, thereby ostensibly giving their offspring the best genes (Alatalo et al. 1992; Duraes et al. 2009). During lek attendance, displaying males congregate at communal breeding areas in habitat with reduced visual obstructions. Displaying males compete for a central display position, which provides dominant males with increased breeding opportunity (DuVal et al. 2018). Sub-dominant males take display positions on the periphery and typically have less breeding opportunities, but still can display for potential mates (DuVal et al. 2018). Females attend leks and observe displaying males to select a mate (Gibson and Bradbury 1985; Nooker and Sandercock 2008). Male investment in breeding and nesting normally does not continue beyond copulation, and females will select nest sites, incubate eggs, and raise broods with little paternal assistance for species that follow this breeding strategy (DuVal et al. 2018; Gibson and Bradbury 1985).

Sagebrush ecosystems provide the necessary conditions for evolution of lek breeding strategies in western North America and several species practice this behavior (Smith et al. 2016; Stiver et al. 2008). These ecosystems are extremely important for many wildlife species; however, fragmentation due to overgrazing, fire management practices, wildfires (Knick and Rotenberry 2000; Wood et al. 2019), and mechanical treatment (Chambers et al. 2014; Smith and Beck 2018) have reduced sagebrush communities and impacted their associated fauna (Knick 1999; Oyler-McCance et al. 2001). These alterations to sagebrush ecosystems reduce and fragment habitats and may have profound impacts on sagebrush obligate species (Edgel et al. 2018; Knick et al. 2003; Pierce et al. 2011). As a result of fragmentation and disturbance,

sagebrush ecosystems in the western United States only occur on a small percentage of their historic distribution (Beck et al. 2012; Decker et al. 2017).

Greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) are a sagebrush obligate species that attends leks for breeding in March through May (Fremgen et al. 2019; Shyvers et al. 2018; Wann et al. 2019). Sage-grouse are native to the western United States and Canada (Knick and Connelly 2011; Smith et al. 2019) and require large, unbroken tracts of sagebrush (*Artemisia* spp.) to meet their year-round habitat needs (Connelly et al. 2000). Part of that year-round habitat includes large areas (3.2 km surrounding lek sites) of breeding habitat that contain leks where males can actively display (Connelly et al. 2000; Row et al. 2018). During breeding season, male movement among leks is rare. Probability of daily movement between leks by males is extremely low, estimated at between 0.3 and 1.0% (Fremgen et al. 2017). Another study in Washington state found that only 25% of male sage-grouse in the study relocated to a different lek in the next year (Schroeder and Robb, 2003). Currently, very little information exists describing how female sage-grouse move while attending leks, although previous genetic work has suggested that females may disperse across breeding habitat located in large tracts of sagebrush (*Artemisia* spp.) steppe ecosystems (Bush et al. 2010; Cross et al. 2017).

Conservation of sage-grouse is dependent on the size and juxtaposition of intact areas of sagebrush habitat for breeding (Coates et al. 2020; Connelly et al. 2000; Dahlgren et al. 2019). Habitat conservation and land-use planning decisions can benefit from identifying how sage-grouse use habitat including breeding areas (Heinrichs et al. 2019; Pratt and Beck 2019). We hypothesized that female sage-grouse would use similar breeding areas across years. We also predicted that female sage-grouse would visit the same breeding areas and leks each year

and that the size of breeding areas would be similar between years. Our objective is to estimate the size of area used by female sage-grouse during breeding season, and determine how female sage-grouse move through breeding habitat and between leks both within and across years. This information will help managers conserve sage-grouse breeding habitat, which will benefit land-use planning.

STUDY AREA

We captured female sage-grouse in three areas in southern Idaho (Fig. 2.1). Our study areas included the Big Desert, the area surrounding Salmon, Idaho, and Sand Creek Desert (Fig. 2.1). Boundaries for each study area followed Bureau of Land Management (BLM) administrative boundaries which were generally consistent with topographic features (e.g., mountain ranges). Each study area consisted of sagebrush-steppe habitat, which was made up of a juxtaposition of dry-land brush communities with more open areas occurring in mesic sites and disturbed areas (Leonard et al. 2000). Mixed/mountain shrub habitat types occurred within moist drainages and on north aspects (Fischer et al. 1997). Elevations in our study areas ranged from 900 to 3,900 m and topography consisted of low rolling hills with higher elevation ranges located on the periphery of suitable sage-grouse habitat. Annual precipitation ranged from 12 to 45 cm (Wakkinen et al. 1992). Common plant species occurring in all study areas were big sagebrush (*A. t. spp.*), antelope bitterbrush (*Purshia tridentata*), green rabbitbrush (*Chrysothamnus viscidiflorus*), crested wheatgrass (*Agropyron cristatum*), blue bunch wheatgrass (*Pseudoroegneria spicata*), bulbous bluegrass (*Poa bulbosa*), yellow salsify (*Tragopogon dubius*), buckwheat (*Eriogonum spp.*), tapertip hawksbeard (*Crepis acuminata*), downy brome (*Bromus tectorum*), and juniper (*Juniperus spp.*). Most of the land in all three study areas was

managed by the BLM with some small, private parcels, and lands managed by the state of Idaho dispersed throughout. Grazing by domesticated cattle (*Bovis* spp.) and sheep (*Ovis aries*) occurred in all three study areas and was administered by the BLM. All three areas contained areas designated as critical sage-grouse habitat in the Idaho Sage-Grouse Management Plan (Otter 2012).

Other animals present in our study area were mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and pronghorn antelope (*Antilocapra americana*). Additionally, several species of predators occurred in our study areas that have been documented to prey on sage-grouse and their eggs. Those predators included red fox (*Vulpes vulpes*), badger (*Taxidea taxus*), coyote (*Canis latrans*), and avian species, such as golden eagle (*Aquila chrysaetos*) and common raven (*Corvus corax*) (Kammerle and Storch 2019; Kirol et al. 2018).

METHODS

Capture, Collaring, and Tracking

At capture, we determined age and sex of sage-grouse, and fitted female sage-grouse with global positioning system (GPS) Platform Transmitter Terminal (PTT) rump-mounted transmitters (22-gram Solar Argos/GPS PTT-100, Microwave Telemetry Inc.). PTT transmitters were programmed to upload six locations per day. The number of actual locations logged per day, however, was less as satellite fixes were not always adequate to generate a GPS location. To quantify the accuracy of PTT transmitters, we placed one transmitter in sage-grouse habitat for 28 days. We also recorded the exact location of that transmitter using an accurate GPS unit (Trimble GEO XH 6000, Trimble Inc., Sunnyvale, California). Mean accuracy for 169 points from that transmitter was 14.3 m (SD \pm 8.6 m, range = 0 to 107 m).

To quantify the number of leks visited by each female during breeding season, we delineated a 250 m buffer around each lek location. We then considered a lek attended if the female was recorded inside the 250 m buffer. We chose 250 m to account for variation in timing of GPS fixes versus when females were on the lek, GPS error, variation in sizes of leks, and the possibility of leks moving locations between years (Harju et al. 2018). Breeding occurred from mid-February to May, and we considered the period of lek attendance for each bird as the time between the first visit to a lek each year and the first visit to that year's nest location. We did not include the first year of breeding season data in our analyses, because we captured female sage-grouse on leks where sage-grouse were, and had been, actively breeding; capture and attachment of transmitters could have affected their behavior during the initial year's breeding season. We retrieved transmitters when GPS locations indicated that a device had stopped moving, due to either the device falling off the bird or mortality. Devices were then located using hand-held UHF receivers (DJ-X11, Alinco inc., Osaka Japan) and 3-element Yagi antennas. We downloaded GPS transmitter data regularly and removed location points with a dilution of precision value of >10 (D'Eon and Delparte 2005; Lendrum et al. 2013) to ensure accuracy of locations.

Data Analyses

We determined the mean male attendance at each lek in our study areas using count data provided by the Idaho Department of Fish and Game. We calculated lek density for each study area by placing our study area outlines over a map of active leks in ArcMap® (Esri, Redlands California, USA) and counting the number of leks present within each study area. To determine density of leks in study areas, we divided the number of leks by the area in km^2 for each study

area. We used (GPS) data from the earliest lek visitation (February 19) to the latest initial visit to a nest site (May 7) to track female sage-grouse through the breeding season to determine size of breeding area (km²) and how many leks females visited. To estimate the size of breeding areas, we calculated 95% brownian bridge estimates using the BBMM package (Nielson et al. 2013) in R (R development core team 2008) for each bird within each year. We determined lek location using an Esri shapefile of leks provided to us by the Idaho Department of Fish and Game compiled from their annual surveys. We documented the number of leks visited by overlaying GPS points gathered for each breeding season with the 250 m lek buffers and counted each lek that the female came within 250 m of during breeding (Harju et al. 2018). To determine if size of space-use while nesting influenced nest success, we performed a Wilcoxon ranked-sum test on consecutive-year breeding attempts. To determine the amount of fidelity to breeding areas, we imported brownian bridge estimates in ArcMap® for the first year and then overlaid the estimate for the second year for each female where two or more years of data was recorded. We then calculated the percent of overlap of those two brownian bridge estimates of space use. We performed Wilcoxon ranked-sum tests to compare sizes of first year and consecutive year brownian bridge estimates (Lam and Longnecker 1983).

To compare factors influencing the size of breeding areas, we used a mixed-effects linear regression model using the lme4 package (Bates et al. 2015) in R. Our response variable was breeding-area size. Our random variables were calendar year (year) and bird id with fixed-effects being study area, number of consecutive years we observed breeding attempts (breeding year), and number of leks visited (Table 2.1). We checked variables for correlation prior to model construction using the cor function in R to verify that no values were greater than |0.6|. To evaluate relative model support, we judged models based on minimization of Akaike's

Information Criterion adjusted for small sample sizes (AICc) and the final model table was screened for uninformative parameters and ranked using AICc weights (Akaike 1973; Arnold 2010; Anderson, 2002; Wagenmakers 2003).

RESULTS

During spring 2015 to 2019, biologists from the U.S. Bureau of Land Management, U.S. Forest Service, and the Idaho Department of Fish and Game captured 234 female sage-grouse at leks using rocket nets ($n = 53$) and spotlighting ($n = 181$) (Wakkinen et al. 1992). After loss of transmitters, mortality in the first year, or insufficient data points, we used data from 50 female sage-grouse across 68 breeding attempts in our analyses. Of those 68, we were able to record 18 consecutive-year breeding attempts. During that time, we also compared size of breeding areas of 18 female sage-grouse between successive years, as well as degree of overlap of breeding areas for those 18 females. Number of documented leks in our study areas were 44 in the Big Desert, 67 in the Salmon study area, and 84 in the Sand Creek Desert. Lek density was 0.006 leks/km² in the Big Desert, 0.007 leks/km² in the Salmon study area, and 0.02 leks/km² in the Sand Creek Desert. The median male attendance at leks was 9 (interquartile range = 2 to 20 males) in the Big Desert, 11 (interquartile range = 6 to 19.5 males) in the Salmon area, and 8 (interquartile range = 3 to 8 males) in the Sand Creek Desert. From 2015 to 2019, we collected 7,810 locations during the breeding season (mean = 95 locations/bird, SD = 79.5 locations, range = 30 to 122 locations) for 50 female sage-grouse across 68 discrete breeding attempts. We recorded the locations and movements during the breeding season for five females in the Big Desert, four in the area surrounding Salmon, and 59 in the Sand Creek Desert. Median size of brownian bridge estimates for breeding areas was 21 km² ($n = 68$ km², interquartile range = 7.8

to 59.3 km²). Across all study areas, each bird visited (within 250 m) a mean of 2 leks each year (SD = 1.2 leks, range = 1 to 6), although each brownian bridge estimate contained an average of 5 leks (SD = 5.5, range 2 to 12).

The global model in our analysis of breeding-area size was the top ranked model and contained 0.45 of the total AICc weight (Table 2.2). There were two competing models in our analysis which contained greater than 0.1 of the total AICc model weight (Table 2.2). Study area was the only variable to appear in all three top models, however, leks visited and breeding year appeared in two of our top three models. All variables in our top model contained zero in their 85% confidence intervals around the β estimate, although number of leks visited was at the edge of the confidence interval (Table 2.3).

For the 18 females with consecutive years of data, brownian bridge estimates were not different in the second year (1st year median = 21.6 km², 1st year interquartile range = 8.0 to 51.5 km², 2nd year median = 24.7km², 2nd year interquartile range = 6.2 to 73.0km², W -value = 61, p -value = 0.49). Of the 18 consecutive-year breeding attempts, only 7 individuals visited the same lek in consecutive years and none had more than one common lek in consecutive years. There was no difference in the size of the brownian bridge estimates in the second year for successful or unsuccessful nests ($n = 18$, W -value = 695, p -value = 0.18). Mean degree of overlap of breeding areas for these 18 females across years was low (median = 32%, mean = 41%, SD = 35%, range = 5% to 100%) (Fig. 2.2).

DISCUSSION

We predicted that female sage-grouse would use similar areas for breeding and that the study area and the number of leks visited would influence the size of breeding area for those breeding attempts. Little support existed, however, for the idea that breeding-area size differed by study area. Nonetheless, reduced capture effort in two of our study areas led to smaller sample sizes, which may have influenced those results. Regardless, breeding area size for females were large (up to 125 km²). Also, we documented that brownian bridge estimates for female sage-grouse during breeding contained a mean of 5 leks, but on average females only visited less than 2 of those leks. These outcomes may have been because females dispersed long distances (8.8 km) (Dunn and Braun 1985), showed breeding preference for dominant males, and moved through large areas to select a dominant male for mating (Dunn and Braun 1985; Plaza et al. 2019). Additionally, those large breeding areas and visits to different leks between years could have aided female sage-grouse in promoting genetic diversity in their offspring (Cross et al. 2017; Row et al. 2018). Current management recommendations suggest a 3.2 km buffer around leks in order to conserve breeding habitat which equates to 32.2 km², however, some research has identified that protection of habitat up to 18 km around leks (1,017.9 km²) may be needed for migratory populations to preserve necessary amounts of breeding habitat (Connelly et al. 2000). Our results indicate that 3.2 km buffers may be insufficient to adequately protect breeding habitat in certain circumstances, however, 18 km buffers would contain the area and leks sufficient to conserve breeding habitats for female sage-grouse in our study areas.

We also predicted that female sage-grouse would visit the same breeding areas and leks each year. The first part of that prediction was upheld as all brownian bridge estimates for female sage-grouse overlapped in successive years. That result is also supported by previous findings

indicating that female sage-grouse have a high level of fidelity to nesting areas, which are closely linked with breeding areas (Berry and Eng 1985; Fischer et al. 1993; Holloran and Anderson 2005). Despite high fidelity to breeding areas, only 39% of females visited the same lek in consecutive years with most not returning to the same lek. Brownian bridge estimates of space use for female sage-grouse contained 2.5 times more leks than were visited in a single year and visitation to these leks could have caused the low fidelity to leks visited in previous years. Also, we only received 4-6 relocations each day for each female sage-grouse, therefore it is possible that a female could have visited a lek and left before a point was recorded within our 250 m buffer. Our results differ from previous research using VHF transmitters, which found that juvenile sage-grouse returned to the lek closest to their nest (Dunn and Braun 1985). We hypothesize that female sage-grouse return to familiar areas each year for breeding, but that they choose different leks to encourage genetic diversity (Bush et al. 2010; Bush et al. 2011). Our hypothesis offers support for the findings of previous research that lek breeding systems exist in part to ensure superior genetic inheritance for offspring (Ivy and Lacy 2012). This result may also be caused by the presence of predators (Boyko et al. 2004; Hartzler 1974), or changing weather—such as snow excluding certain areas from use (Bradbury et al. 1989; Fremgen et al. 2019). Our result also demonstrates the importance of preserving areas that populations of female sage-grouse use for breeding as it may be difficult to encourage recolonization of breeding habitat.

We predicted that female sage-grouse would use breeding areas of a similar size between years. Estimates of space-use for 18 female sage-grouse in their second year were similar to estimates from their first (1st year median = 21.6 km², 1st year interquartile range = 8.0 to 51.5 km², 2nd year median = 24.7km², 2nd year interquartile range = 6.2 to 73.0km², *W*-value = 61, *p*-

value = 0.49). In previous research, weather and predators were factors influencing breeding behavior in sage-grouse (Boyko et al. 2004; Bradbury et al. 1989; Fremgen et al. 2019; Hartzler 1974); however, our data were collected over five years and therefore weather or predators likely did not influence our results. We hypothesize that females return to the same areas each year to promote survivorship through familiarity with the area (Beletsky and Orians 1991; Yezerinac et al. 2013). Our result contradicts previous research identifying female dispersal (Cross et al. 2017), which documented sage-grouse dispersal distances from 13 to 127 km from their natal breeding areas.

While information on the movements between leks and size of breeding areas for female sage-grouse has meaningful management implications, there are also some limitations. First, the time interval between GPS relocations was likely too large to capture all visits to leks. Our broader definition of visitation to include any locations within 250 m of leks helps offset this limitation, but we still likely missed some visits (Harju et al. 2018). Also, because sage-grouse were captured in the spring while attending leks, we limited our analysis to sage-grouse that survived a full year. This decision coupled with removal of some individuals due to lack of sufficient GPS data reduced our sample sizes to 68 breeding attempts and limited the number of variables we could include in our models. Also, we did not have meaningful vegetation data to include in our research which is known to have a significant impact on seasonal habitat use and size of space-use (Connolly et al. 2000). Future research on this topic should include GPS transmitters that could reliably support a shorter time interval between relocations for increased accuracy and should examine the impact of habitat variables on movements and space-use during the breeding season.

With the increased attention given to sage-grouse in recent years, emphasis has been placed on identifying important annual habitat, because research has indicated that habitat loss is a driving factor in population declines (Connelly and Braun 1997; Walker et al. 2007). Factors associated with habitat loss include overgrazing, fire management practices, and mechanical or chemical treatment of sagebrush (Chambers et al. 2014; Knick and Rotenberry 2000; Smith and Beck 2018; Wood et al. 2019). Preservation of leks and breeding habitat is an important part of conservation for this species (Connelly et al. 2000; Hess and Beck 2012). We documented that female sage-grouse used large areas while breeding and that they demonstrated high fidelity to breeding areas, but not leks in those areas. We also found no difference in the size of area used by female sage-grouse while breeding in consecutive years. Additional understanding of the movements and space-use of breeding female sage-grouse would provide valuable information for managers seeking to preserve both this species and its habitat. Our results further emphasize the importance of managing sage-brush steppe ecosystems so as to be suitable for sage-grouse during the annual breeding season.

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FIGURES



Figure 2.1: Study areas in Idaho, USA, where we quantified size and fidelity of breeding areas for 50 female greater sage-grouse (*Centrocercus urophasianus*) from 2015 to 2019.

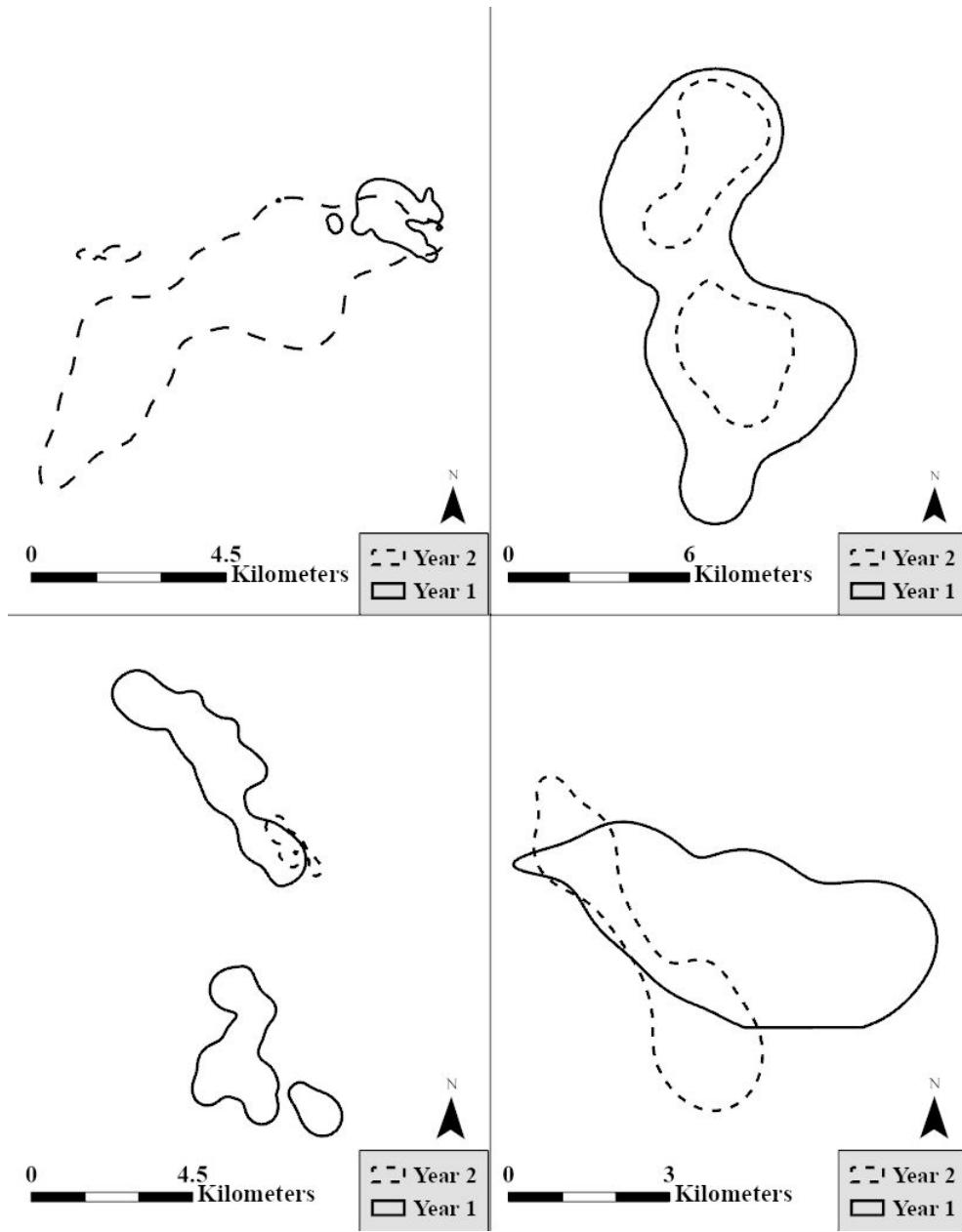


Figure 2.2: Examples of overlap of consecutive year brownian bridge estimates for breeding-area size used by female greater sage-grouse (*Centrocercus urophasianus*), southern Idaho, USA, 2015-2019.

TABLES

Table 2.1: Name and description of variables used to build models for our analysis of size of breeding areas used by female greater sage-grouse (*Centrocercus urophasianus*), southern Idaho, USA, 2015-2019.

Variable Name	Description
Breeding area size	Size (in km ²) of area used by female sage-grouse estimated from a 95% brownian bridge analysis
Breeding year	Whether the data was the 1 st year, 2 nd year, etc. observing that female sage-grouse
Leks visited	Number of leks visited by female sage-grouse during the breeding season in a given year
Study area	The study area where the breeding attempt occurred
Year	Calendar year in which the nesting attempt occurred
Bird id	ID number assigned to each bird

Table 2.2: Model rankings (AICc and Δ AIC), model weights (w_i), number of estimated parameters (K), and log likelihood (LL) for supported models (model weight $\geq 1\%$) of greater sage-grouse (*Centrocercus urophasianus*) breeding area size, southern Idaho, USA, 2015-2019.

Model	Structure	AICc	Δ AIC	w_i	K	LL
m1	Breeding year + leks visited + study area	598.2	0.00	0.451	4	-291.16
m6	Breeding year + study area	600.3	2.09	0.158	3	-293.45
m7	Leks visited + study area	600.3	2.11	0.157	3	-293.46
m8	Breeding year + leks visited	601.3	3.15	0.094	3	-293.98
m3	Study area	602.4	4.2	0.055	2	-295.71
m4	Breeding year	603.1	4.87	0.039	2	-296.05
m5	Leks visited	603.5	5.27	0.032	2	-296.24
m2	Null model	605.3	7.09	0.013	0	-298.32

Table 2.3: Parameter estimates for variables included in our top model for analysis of breeding-area size in female greater sage-grouse (*Centrocercus urophasianus*). We report estimates, standard error (s.e.), lower (L85CI) and upper (U85CI) confidence intervals, Z-values and *p*-values.

Parameter	Estimate	s.e.	L85CI	U85CI	Z-value	<i>p</i> -value
Intercept	32.62	12.067	11.650	49.640	2.514	0.034
Big Desert	2.98	4.384	-2.670	12.621	0.842	0.584
Salmon Area	-0.22	3.844	-2.754	19.637	0.923	0.438
Breeding year	-0.29	3.567	-6.100	5.400	0.079	0.937
Leks visited	-1.89	2.090	-5.360	0.730	0.890	0.374