

Linking microhabitat selection, range size, reproductive state, and behavioral state in greater sage-grouse

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Abstract

A female's reproductive status influences her behavior which affects habitat selection and range size; however, reproduction and behavior are generally unaccounted for in habitat selection studies. Range size, daily activity, and habitat selection between reproductive states have rarely been investigated in a connected manner. We focused on brood-rearing and broodless (i.e., females without young) greater sage-grouse (*Centrocercus urophasianus*). Our objectives were as follows: 1) identify differences between reproductive state (females with broods 0–2 weeks, broods 3–5 weeks, and broodless females) and behavioral state (foraging, day roosting, and night roosting) in microhabitat selection, 2) evaluate daily activity for brood-rearing and broodless females, and 3) contrast daily and seasonal range sizes for each reproductive state. We collected Global Positioning System location and accelerometer data every 5 min from female sage-grouse in Carbon County, Montana, and Park County, Wyoming, USA, in 2018–2019. We sampled microhabitat for 36 females at 276 bird-use and random plots, estimated ranges for 38 females, and measured activity for 43 females. Females with broods 0–2 weeks selected against visual obstruction and for perennial grasses at night roosts, females with broods 3–5 weeks selected for visual obstruction when foraging and against visual obstruction and annual grasses but for sagebrush cover at night roosts; however, broodless females showed no selection. Patterns of daily activity differed between females with broods 0–2 weeks and broodless females; females with

broods 3–5 weeks showed an intermediate pattern. Females with broods 0–2 weeks had the smallest daily (0.027 km²) and seasonal (0.21 km²) ranges compared with females with broods 3–5 weeks (daily = 0.038 km², seasonal = 0.36 km²) and broodless females (daily = 0.035 km², seasonal = 0.44 km²). Our results indicated the importance of considering reproductive and behavioral state and accounting for habitats and space required by all individuals in conservation and management decisions.

KEYWORDS

activity, broodless, brood-rearing, *Centrocercus urophasianus*, habitat, resource selection

Understanding how reproductive state influences behavior, which in turn influences habitat selection and range size has important implications for effective management by improving our understanding of how animals use landscapes. During the breeding season, reproductive state (i.e., caring for young or not; Mackie and Racey 2007, Smith et al. 2018, Viejou et al. 2018) affects behavior (e.g., resting or foraging; Roever et al. 2014). Behavior then influences habitat selection, range size (van Beest et al. 2011), and an animal's activity patterns (e.g., time when active; Walker et al. 2006) throughout the day. Females with young have a greater need to avoid risky habitat and prioritize their offspring's safety by more strongly avoiding predation risk than females without young (Viejou et al. 2018), therefore increasing the amount of time using safe habitats (Brown 1999). Moreover, reproductive state influences habitat selection in numerous species, for example, noctule bats (*Nyctalus noctule*; Mackie and Racey 2007), blue crabs (*Callinectes ornatus*; Segura de Andrade et al. 2014), and greater sage-grouse (*Centrocercus urophasianus*; Smith et al. 2018). Nonreproductive females may use a greater variety of habitat (Rayment et al. 2015, Smith et al. 2018), use the same habitat but for a different amount of time (Mackie and Racey 2007), or use different size ranges (Dahle and Swenson 2003, Henry et al. 2005, van Beest et al. 2011) than their counterparts with young. Differences in range sizes may be due in part because nonreproductive females are more mobile than females with young (Thiebot et al. 2011) and can thus access a greater area and greater diversity of habitat. Reproductive state may also influence a female's activity levels throughout the day. For example, females without young can spend more time in reduced activity than their reproductive counterparts who must remain vigilant to reduce predation risk for themselves and their young or remain active to increase time spent foraging.

A female's behavioral state changes throughout the day and is influenced by her reproductive state. Females may change their behavior to become more vigilant for foraging, for resting, or for moving from one habitat patch to another depending on the time of day. Different behavioral states influence a female's activity levels and time spent in each activity. Females expressing different behavior may show differences in habitat selection throughout the day (Roever et al. 2014) as suggested by previous research showing differences in sage-grouse habitat selection during different times of the day (Dunn and Braun 1986, Sveum et al. 1998), at night (Dzialak et al. 2011), and within and between patches (Dzialak et al. 2015). Aside from changing behavioral state, the time spent therein may change throughout the day (Walker et al. 2006). Additionally, different behavioral states or time spent therein may influence range size; for example, resting animals with low activity may utilize smaller ranges than when animals are actively foraging (Christiansen et al. 2017).

Assessing how behavioral state affects habitat selection can provide important insight and better understanding into species-habitat relationships compared to studies that do not account for various behaviors (Beyer et al. 2010, Roever et al. 2014). Selection for or against specific habitat components may differ depending

upon the animal's behavior, sometimes resulting in identifying different selection patterns depending on whether behavior is accounted for in models (Roever et al. 2014). Even between reproductive states, behaviors can impact habitat use and the amount of time spent within certain habitat features (Walker et al. 2006). Incorporating daily behavior into habitat selection analyses can elucidate habitat selection by highlighting different habitats used during different behaviors or different selection patterns that other studies that do not account for behavior are unable to do. However, though accounting for behavior is important, it has received relatively little attention because much of the location data used by many telemetry studies with few locations lacks a behavioral component (Beyer et al. 2010). Advanced Global Positioning System (GPS) technology, tri-axial accelerometer data, and high frequency rates of location fixes can help distinguish between animal behaviors that were once only possible through direct observation (Wilmers et al. 2015). Behaviors such as walking, resting, foraging, swimming, and grooming have been revealed using GPS and accelerometer data in a variety of species (e.g., Yoda et al. 2001, Graf et al. 2015, Wang et al. 2015), including birds (Nathan et al. 2012).

Greater sage-grouse (hereafter, sage-grouse) is a species of conservation concern that has undergone substantial range contraction and population decline (Schroeder et al. 2004, Nielson et al. 2015). Greater sage-grouse were considered warranted, but precluded for listing in 2010 under the Endangered Species Act due to habitat loss, fragmentation, and lack of regulatory mechanisms (U.S. Fish and Wildlife Service 2010). Declines in populations and concern about habitat loss and degradation have prompted a considerable number of studies on sage-grouse, such that habitat selection during the breeding season by brood-rearing females has been well studied (Drut et al. 1994, Dinkins et al. 2012, Kirol et al. 2012, Mabray and Conover 2015). Both female and chick survival are important vital rates for sage-grouse population growth (Taylor et al. 2012) even though sage-grouse are a relatively long-lived galliform with low reproductive output (Connelly et al. 2011). Due to variation in sage-grouse productivity across years from environmental stochasticity (Taylor et al. 2012), survival of broodless females (i.e., females without a brood) may become even more important during years of low reproductive success. Different sage-grouse reproductive states can influence habitat selection (Gregg et al. 1993, Kirol et al. 2015, Smith et al. 2018) but little is known about how sage-grouse behavior influences habitat selection (but see Dzialak et al. 2015).

The concern for sage-grouse populations and need for conservation of their habitat make sage-grouse an ideal candidate for studying the links between reproductive and behavioral state effects on habitat selection, range size, and daily activity. Although previous studies have examined breeding season habitat selection (Drut et al. 1994, Thompson et al. 2006, Mabray and Conover 2015, Smith et al. 2018) and range size (Drut et al. 1994) separately, or reproductive state influence on habitat selection (Mabray and Conover 2015, Smith et al. 2018) these studies did not account for behavioral state nor examined reproductive state influence on daily activity and range. We chose to examine 3 reproductive states based on differences in habitat selection between females with broods 0–2 weeks and 3–5 weeks (Thompson et al. 2006, Kirol et al. 2012, Kirol et al. 2015, Smith et al. 2018) and between brood-rearing and broodless female sage-grouse (Smith et al. 2018). The goal of our study was to understand the links between reproductive state, behavioral state, habitat selection, range, and daily activity to help elucidate how behavioral and reproductive state influence how sage-grouse utilize their landscape. Our objectives were as follows: 1) identify differences between reproductive states (females with broods 0–2 weeks, broods 3–5 weeks, and broodless females) and behavioral states (foraging, day roosting, and night roosting) in third-order habitat selection (i.e., microhabitat; Johnson 1980); 2) examine the effect of reproductive state on daily activity; and 3) examine the influence of reproductive state on daily and seasonal range sizes. We predicted sage-grouse would select for less cover when night roosting and greater forb cover when foraging (Table 1; Drut et al. 1994, Fedy et al. 2014), differentiating their selection based on behavior. Similarly, we predicted brood-rearing females would choose areas with less cover and more forbs compared with broodless females who would select a greater variety of habitats (Smith et al. 2018). We predicted activity levels would differ during the day between reproductive states, such that brood-rearing females would take longer to become active in the morning and be more active during the day to satisfy nutrient requirements of the chicks whereas broodless females would show more variable activity levels throughout the day (Maxson 1974). We also predicted brood-rearing females would have smaller ranges than broodless females due to mobility constraints of having chicks.

STUDY AREA

Our study area was approximately 487 km² located in southern Carbon County, Montana and northern Park County, Wyoming (from 109°3'57.6"W 45°10'33.6"N to 109°4'55.2"W 44°57'28.8"N). Elevation ranged from 1158–2080 m above sea level. Annual mean high temperature was 13.5°C and 12.3°C (30-year average was 12.6°C from 1981–2010), mean minimum temperature was -0.9°C and -1.5°C (30-year average was -0.6°C from 1981–2010), and mean precipitation was 35.5 cm and 40.5 cm (30-year average was 42.0 cm from 1981–2010) in 2018 and 2019, respectively (PRISM Climate Data; <http://www.prism.oregonstate.edu>). Exurban residential development, cattle grazing, and recreational use all occurred within the study area. Anthropogenic development was primarily houses or agricultural fields and associated buildings with some small areas of oil and gas infrastructure. Within the study area, 61% was public land (54% Bureau of Land Management, 3% U.S. Forest Service, and 4% State Trust) and 39% was private land. The landscape was dominated by basin big sagebrush (*Artemisia tridentata tridentata*) and Wyoming big sagebrush (*A. t. wyomingensis*). Other common shrubs in the study area included black sagebrush (*A. nova*), broom snakeweed (*Gutierrezia sarothrae*), Gardner's saltbush (*Atriplex gardneri*), greasewood (*Sarcobatus vermiculatus*), rubber rabbitbrush (*Ericameria nauseosa*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), and shadscale saltbush (*A. confertifolia*). Isolated stands of juniper (*Juniperus spp.*) were found on steeper hillsides or at higher elevation. Dominant perennial grasses included blue grama (*Bouteloua gracilis*), Indian ricegrass (*Achnatherum hymenoides*), needle-and-thread (*Hesperostipa comata*), and Sandberg bluegrass (*Poa secunda*). Cheatgrass (*Bromus tectorum*) was abundant throughout a majority of the study area.

METHODS

We captured female sage-grouse from the Montana portion of our study area in spring and summer of 2018 and 2019 across 7 leks during spring or near GPS-tagged birds in the summer. We captured sage-grouse at night using spotlighting and hoop-netting techniques (Giesen et al. 1982). We fitted sage-grouse with solar-powered, rump-mounted transmitters (15g-Bird Solar tag, e-obs GmbH, Grunwald, Germany, with attached 6g-VHF tag, Holohil, Ontario, Canada; total weight ~30 g including harness material) collecting location and accelerometer data every 5 minutes during daylight and some nighttime hours (0330–2300 MDT). We collected data from the remote-download transmitters weekly to monitor the status of each female by examining their locations and movement patterns. We examined GPS locations to monitor the time and day each female grouse completed nesting, with brood-rearing beginning when the female moved from a successful nest without returning. We monitored nests for success or failure, with a successful nest hatching at least one egg, as determined by examining the eggshell for a detached membrane (Wallestad and Pyrah 1974). We monitored broods until 5 weeks posthatch by examining movement data to ensure females still had chicks. We searched specifically for evidence a female flew long distances or flew off a night roost (without quickly returning), with a large flight (>100 m when chicks were <2 weeks old) indicative of a broodless female (Dzialak et al. 2011). We used 35 d posthatch as the conclusion of brood-rearing success because the majority of chick mortality occurs before 35 d (Gregg et al. 2007). In addition, we checked all broods 2 weeks posthatch by going to the previous night's roost based on the female's locations and examining the roost for chick droppings (presence of chick droppings indicating the female had a brood) while eliminating any disturbance to the brood. If a female was suspected to have lost her brood within the 5-week window, we immediately verified by locating and flushing the female at night. We determined the success of each brood-rearing female at 35 d posthatch by checking the female at night, with the presence of at least one chick with the female signifying brood success (Kirol et al. 2015). If either of the physical checks on brood status contradicted our estimated status based on movement data, we checked the female grouse again the following night to confirm brood status. After physical brood checks, the status of every brood matched our estimated status based on

movement data. If a female was confirmed to have lost her chicks or her nest failed with no subsequent re-nest, we censored this female for one week before she was considered a broodless female to ensure she completely transitioned behavior, movement, and habitat selection. Females that never nested were considered broodless starting on 15 May of each year. We monitored broodless females until they either moved to summer range (usually irrigated hayfields or pastures) or the last brood reached 5-weeks posthatch, whichever occurred first.

Microhabitat selection

We separated brood-rearing females into 2 categories, 0–2 weeks (d 1–14) and 3–5 weeks (d 15–35) posthatch, due to differences in habitat use shown for these 2 brood periods (Thompson et al. 2006, Kirol et al. 2012, Kirol et al. 2015, Smith et al. 2018). We focused on 3 reproductive states for analyses: females with broods 0–2 weeks, broods 3–5 weeks, and broodless females. To examine behavioral state influence on microhabitat selection of brood-rearing and broodless females, we sampled vegetation at locations associated with foraging and roosting. We separated out the activities to include one foraging, one day roost, and one night roost location, basing each of the locations on the behavior of a unique sage-grouse for one day. We determined each used point for vegetation sampling based on GPS locations and accelerometer data collected by the transmitters. We collected accelerometer data once each 0.1 sec over a 10-sec sampling period every 5 min on X, Y, and Z axes. We used the variance in acceleration measured over the 10-sec period along the Z-axis to quantify activity levels because this axis changed the most with bird movement. We calculated location-specific nautical dawn/dusk and sunrise/sunset to aid in defining foraging and day roosting points (suncalc R package; Hieurmél and Elmarhraoui 2019, R Core Team 2020). For the foraging points, we were attempting to identify foraging behavior by selecting the locations when the birds were most active for an extended time (minimum 10 min) without moving the farthest distances. For day roost points, we were attempting to identify day roosting behavior by selecting locations when the birds were inactive for an extended time (minimum 10 min) and not moving. We defined foraging points for sampling as locations where the variance in measured acceleration was within the highest 25th quartile measured that day and the average of the previous and subsequent locations within 10 min (median over a 20-min window) was also within the highest 25th quartile. Foraging locations had to be between nautical dawn (~0400–0430 MDT) and dusk (~2200–2230 MDT). Besides having a high variance in acceleration, foraging points also needed a step length (i.e., distance between previous and subsequent locations) that was not an outlier (i.e., less than the 75th quartile + 1.5 times the interquartile range) of all the distances recorded for that bird-day. Using these criteria, we were attempting to identify locations when grouse were active but not flying or walking/running quickly in a straight line. We identified day roost points by distance moved and acceleration variance in the lowest 25th quartile for the location and the average of locations within the 20-min window. Day roost locations could occur at any time during the day within one hour after sunrise and one hour before sunset. We identified night roosts by randomly selecting between the first (0330 MDT) and last (2300 MDT) GPS locations recorded that day, which were before nautical dawn or after nautical dusk. For night roosts, we ensured the female had not been flushed earlier in the night by checking the female's locations. We ensured each bird-use location was based on behavior of the grouse, foraging or roosting, so time of day of each location varied.

We paired each of the individual bird-use locations (foraging, day roost, and night roost) with one random location, therefore we considered these 3 sets to be paired microhabitat plots. We created a minimum convex polygon (MCP) based on all the female's locations for that day and selected a random location within that MCP to use as the paired-random plot to compare microhabitat to each of the used locations. In this way the female could have selected the paired-random plot as it was available within her daily home range (Jones 2001). We set all plots a minimum of 40 m apart, hence, no plots could overlap, and the random plot could not overlap any of the bird's locations and was therefore unused on that day. We completed no more than 2 paired microhabitat plots per each reproductive state-bird-year (Smith et al. 2018). We sampled all vegetation for bird use and paired random plots

within 7 d of use by the female to accurately capture microhabitat vegetation used by the female. Some ($n = 28$; 43.7%) females were not sampled for microhabitat characteristics due to logistical constraints, the female died before having a brood, or the female died before we were able to sample vegetation used by the female.

We sampled microhabitat-scale (30 m \times 30 m) or third-order habitat selection (Johnson 1980) vegetation characteristics at each bird-use and random plot including shrub cover, herbaceous cover, ground cover, and visual obstruction. For each plot, we collected vegetation measurements along 4, 15-m transects radiating out in cardinal directions from the center of each plot. At each plot we measured biologically relevant variables important for sage-grouse during the brood-rearing season (Table 1). We used the line intercept method across all 4 transects resulting in 60 m total for each plot to estimate shrub canopy cover by species (Canfield 1941). We measured visual obstruction by averaging 26 Robel pole readings per plot, taking 2 readings at 5, 10, and 15 m in each cardinal direction from plot center and 2 readings at plot center (Robel et al. 1970). Each Robel pole reading was taken in the opposite direction along the transect lines. We assessed herbaceous and ground cover within 17, 0.1-m² (20 \times 50 cm) Daubenmire

TABLE 1 Variables considered in habitat selection models and predicted response with citations for each variable for greater sage-grouse in Carbon County, Montana, and Park County, Wyoming, USA, 2018 and 2019. Variables were screened for correlation and variance inflation factors before building initial models.

Variable	Description	Predicted response	Citation
Sagebrush	Sagebrush cover from line intercept (%)	Select against when night and day roosting for brood-rearing females; select for when foraging	Kirol et al. 2012
Shrub ^a	Shrub cover from line intercept (%)	Select against when night and day roosting for brood-rearing females, select for females with broods 3–5 weeks	Smith et al. 2018
Annual grass ^b	Mean annual grass cover from Daubenmire quadrats (%)	Select against by all behavioral and reproductive states	Kirol et al. 2012 (documented selection against for nests)
Perennial grass	Mean perennial grass cover from Daubenmire quadrats (%)	Select for by all behavioral and reproductive states	Kirol et al. 2012
Residual grass ^c	Mean residual grass cover from Daubenmire quadrats (%)	Select against by females with broods 0–2 weeks	Smith et al. 2018
Forb	Mean forb cover from Daubenmire quadrats (%)	Select for when foraging	Drut et al. 1994
Food forb ^a	Mean sage-grouse food forb cover from Daubenmire quadrats (%)	Select for when foraging for all reproductive states	Drut et al. 1994, Kirol et al. 2012, Smith et al. 2018
Forb species richness	Forb species richness from Daubenmire quadrats (no.)	Select for when foraging for all reproductive states	Smith et al. 2018
Litter ^a	Mean litter cover from Daubenmire quadrats (%)	Select for by broodless females, no selection by brood-rearing females	Smith et al. 2018
Visual obstruction	Visual obstruction estimated from Robel pole (dm)	Different selection depending on behavior, select by females with broods 0–2 weeks and broodless females	Schreiber et al. 2015, Smith et al. 2018

^aDropped from analyses after initial screening based on correlation and VIF coefficients.

^bAnnual grass consisted of mostly cheatgrass with some (<5%) field brome (*B. arvensis*).

^cResidual grass was defined as the standing, dead perennial grass leaves from the previous year.

quadrats equally spaced at 3.75-m increments from the center along all transects and one at the center of each plot (Daubenmire 1959). We defined percent cover within each Daubenmire quadrat using the following cover classes: 1 = 0–1%, 2 = 1.1–5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, and 6 = 75.1–100%. We grouped forbs considered to be eaten by sage-grouse together as food forbs (see Kiol et al. 2012), whereas all other forbs we considered non-food. We tabulated forb species richness as the number of species of forbs (both food and non-food) found in each plot. More details about methodology to collect microhabitat vegetation data information at each location are found in Kiol et al. (2012) and Dinkins et al. (2016).

We employed a modified Design IV from Erickson et al. (2001) to analyze microhabitat characteristics at both use and available locations for individual grouse, resulting in paired use-available data. We paired each bird-use location (foraging, day roost, night roost) with one random location for analyses. Due to logistical constraints, we used the same available location per behavioral state, for example, for one female we sampled 4 microhabitat plots per day including one day roost, night roost, foraging, and available plot. We modeled microhabitat selection using a binomial conditional logistic regression model with a use-available design (survival R package; R Core Team 2020, Therneau 2020), where we considered bird-use plots as used and paired-random plots as available. We modeled each behavioral state (foraging, day roost, night roost) and reproductive state (females with broods 0–2 weeks, broods 3–5 weeks, and broodless) separately. We evaluated quadratic expressions for cover variables but found they did not improve model fit. We also did not include interactions due to small sample size. We accounted for repeated sampling of the same individual by using Bird ID as a random effect. We checked for collinearity by using a Pearson correlation matrix—any variable with a correlation coefficient greater than 0.6 or variance inflation factor (VIF, Menard 1995) coefficient greater than 3 was removed. When 2 variables were correlated, we retained the variable that we considered more biologically relevant. We checked all variables for each model for potential outliers (Hosmer and Lemeshow 2000). We conducted model selection using quasi-likelihood under the independence model criterion that accounts for repeated sampling of the same individuals (QIC; Pan 2001, Craiu et al. 2008). We limited models to less or equal to 3 variables to prevent overfitting of our data due to sample sizes. We then model averaged using models with $\Delta\text{QIC} < 4$ from the top model. We validated top models by checking residual plots for normality and outlier influence on data. We considered variables to be biologically and scientifically significant when 95% confidence intervals did not overlap zero.

Activity

We evaluated times of activity (i.e., times when females were active) throughout the day between females with broods 0–2 weeks (d 0–14), females with broods 3–5 weeks (d 15–35), and broodless females. We were not limited by logistical constraints in obtaining activity data as we were with sampling microhabitat, therefore our sample size for activity was larger than for the microhabitat analysis. We reduced locations of broodless females to a random, consecutive 3-week timeframe to be comparable with females with broods 0–2 weeks and 3–5 weeks because these females may be broodless for a few days up to numerous weeks. We only included broodless females in analyses 7 d after losing a nest with no subsequent re-nest, 7 d after losing a brood, or 15 May of each year for females that never nested. We stopped using locations for activity analyses once a broodless female moved from her breeding area towards summer range or 31 July, the latest date all broods would have reached 5 weeks, whichever occurred first to ensure brood-rearing and broodless female locations and timeframes were comparable. Brood-rearing females may have lost their brood during weeks 0–2 or weeks 3–5, hence the actual number of days in each reproductive state may have been less than 2 weeks for females with broods 0–2 weeks or 3 weeks for females with broods 3–5 weeks.

We defined active behavior (which also included both flying and walking besides foraging behavior as described earlier) as when the variance in acceleration measured along the Z-axis was within the highest 25th quartile measured every 5 min and averaged over a 20-min moving window (from 0330 MDT to 2300 MDT). We wanted to

compare the pattern of activity between reproductive states, therefore, we calculated the proportion of bird-days that met this criterion at each of the 5-min sampling periods.

Daily and seasonal ranges

We assessed both daily and seasonal range size (km²) by reproductive state using a dynamic Brownian Bridge Movement Model (BBMM; Kranstauber et al. 2012). Dynamic BBMMs do not have assumptions of independence of points as do some home range models and recognize behavioral change along animal tracks to more accurately describe space use compared with regular BBMMs (Kranstauber et al. 2012). We used a window size of 9 locations and a margin of 3 locations to create the dynamic BBMM (Pratt et al. 2017). We calculated a daily range size for each individual as the mean of daily ranges measured over 2 weeks for females with broods 0–2 weeks old, 3 weeks for females with broods 3–5 weeks old, and 3 weeks for broodless females. We calculated individual seasonal ranges from all locations observed over the same time periods. We used the same dataset and criteria for including brood-rearing and broodless females in analyzing range sizes as for the activity analysis. However, females in any reproductive state with fewer than 8 d of locations were excluded from analyses to ensure an adequate number of days of locations to measure seasonal home ranges.

We estimated daily and seasonal range size based on a 95% utilization distribution calculated from a dynamic BBMM (move R package; Kranstauber et al. 2020, R Core Team 2020). We used a Welch Test (onewaytests R package; Dag et al. 2018, R Core Team 2020), which is an alternative to an ANOVA for data that does not have equal variances (Levene's Test, daily range sizes $P = 0.207$ and seasonal range sizes $P = 0.006$; Kohr and Games 1974, car R package, Fox and Weisberg 2019, R Core Team 2020), to determine whether a difference in daily and seasonal range size existed between reproductive states. To understand which reproductive states differed in range size, we used a Games-Howell test (userfriendlyscience R package; Peters 2018, R Core Team 2020). We set statistical significance at $\alpha = 0.05$.

RESULTS

We monitored 39 female sage-grouse including 17 with broods and 22 broodless females in 2018 and 43 females including 19 with broods and 24 broodless females in 2019. At 5-weeks posthatch, there were 10 (58.8%) successful broods (minimum of one chick remaining at 5 weeks) in 2018 and 11 (57.9%) successful broods in 2019. By the end of the breeding season, broodless females accounted for 60.7% and 60.6% of all living females in 2018 and 2019, respectfully.

Microhabitat selection

We sampled microhabitat vegetation characteristics from 36 unique females at 276 plots, of which 207 were bird-use and 69 were paired-random plots (Table 2). Microhabitat surveys for bird-use and paired-random plots were completed from 20 May to 30 June for females with broods 0–2 weeks, 4 June to 17 July for females with broods 3–5 weeks, and 10 June to 24 July for broodless females. Median brood age at the time plots were identified for microhabitat sampling was 7 d posthatch (range = 2–14 d) for broods 0–2 weeks and 28 d posthatch (range = 18–34 d) for broods 3–5 weeks. We found several competing models for each reproductive state and behavior, therefore, we model averaged the competing models within 4 Δ QIC for each behavior and reproductive state (Table 3, Tables S1–S3, available online in Supporting Information).

TABLE 2 Number (*n*) of 30 × 30-m microhabitat plots completed for each behavioral state (foraging, day roost, night roost) and reproductive state (females with broods 0–2 weeks, broods 3–5 weeks, broodless) for greater sage-grouse in Carbon County, Montana, and Park County, Wyoming, USA, 2018 and 2019.

Reproductive state	Females (<i>n</i>) ^a	Microhabitat plots				Total (<i>n</i>)
		Foraging (<i>n</i>)	Day roost (<i>n</i>)	Night roost (<i>n</i>)	Paired-random (<i>n</i>)	
Broods 0–2 wks	14	22	22	22	22	88
Broods 3–5 wks	18	22	22	22	22	88
Broodless	19	25	25	25	25	100

^aSamples represent unique females in each reproductive state (both for 2018 and 2019 combined); however, individual females could have been sampled in more than one reproductive state.

Females with broods 0–2 weeks and 3–5 weeks selected microhabitat characteristics at night roosts, but only females with broods 3–5 weeks selected for or against specific characteristics when foraging (Table 3, Figure 1). We documented no significant selection across all reproductive states when day roosting. Females with broods 0–2 weeks selected against visual obstruction and for perennial grasses when night roosting but showed no selection when day roosting or foraging (Figure 2). Females with broods 3–5 weeks selected against visual obstruction and annual grass but for sagebrush cover when night roosting. Females with broods 3–5 weeks selected for visual obstruction and forbs when foraging but showed no selection when day roosting (Figure 1). Broodless females showed no selection of any habitat characteristics during any behavioral state.

Activity

We examined daily activity from 43 unique females spanning 1,317 bird-days across reproductive states, resulting in 424 bird-days from 29 females with broods 0–2 weeks, 418 bird-days from 22 females with broods 3–5 weeks, and 475 bird-days from 25 broodless females. Females with broods 0–2 weeks had the largest proportion of bird-days active at 0905 MDT, females with broods 3–5 weeks at 2110 MDT, and broodless females at 2105 MDT (Figure 3). A greater proportion of females with broods 0–2 weeks became active later in the morning, maintained higher activity during the middle of the day, and a smaller proportion were active in the evening compared with broodless females. A smaller proportion of broodless females were active during the day and a greater proportion were active in the morning and evening. Females with broods 3–5 weeks showed a pattern that was intermediate between that of females with broods 0–2 weeks and broodless females.

Daily and seasonal ranges

We analyzed daily and seasonal range size from 27 females with broods 0–2 weeks, 22 females with broods 3–5 weeks, and 23 broodless females spanning 2018–2019 from 39 unique individuals. There were 24 individual grouse that appeared in more than one reproductive state. Mean daily range sizes were 0.027 km² for females with broods 0–2 weeks, 0.038 km² for females with broods 3–5 weeks, and 0.035 km² for broodless females ($F_{2,42} = 8.27$, $n = 69$, $P \leq 0.001$; Table 4, Figure 4). Mean seasonal range size was 0.21 km² for females with broods 0–2 weeks, 0.36 km² for females with broods 3–5 weeks, and 0.44 km² for broodless females ($F_{2,37} = 19.76$, $n = 69$, $P \leq 0.001$). Broodless females had mean daily ranges that were 1.3-times larger than that of females with broods 0–2 weeks ($t_{df=9,83} = 2.79$, $P = 0.021$) and mean seasonal ranges that were 2.1-times the size of females with broods

TABLE 3 Model-averaged estimates and 95% confidence intervals (CI) for variables in the top models for each behavioral state (foraging, day roost, night roost) and reproductive state (females with broods 0–2 weeks, broods 3–5 weeks, and broodless). Estimates with no values indicate that variable did not appear in the final model. Based on microhabitat characteristics at greater sage-grouse bird-use and paired random locations in Carbon County, Montana, and Park County, Wyoming, USA, 2018 and 2019.

Variable	Broods 0–2 weeks					
	Foraging		Day roost		Night roost	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Sagebrush	-0.03	-0.13 to 0.08	0.04	-0.12 to 0.19	0.03	-0.08 to 0.15
Visual obstruction	-0.76	-2.23 to 0.71	-1.67	-4.16 to 0.83	-2.02 ^a	-3.92 to -0.13
Annual grass	0.01	-0.14 to 0.15	-0.16	-0.42 to 0.09	-0.22	-0.51 to 0.07
Perennial grass	0.12	-0.06 to 0.29	0.13	-0.03 to 0.28	0.19 ^a	0.00 to 0.37
Residual grass	0.01	-0.15 to 0.17	0.04	-0.15 to 0.23	-0.18	-0.53 to 0.17
Forb species richness	0.12	-0.12 to 0.36	0.09	-0.17 to 0.35		
Forb	0.04	-0.11 to 0.18	-0.12	-0.36 to 0.13		
Variable	Broods 3–5 weeks					
	Foraging		Day roost		Night roost	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Sagebrush	-0.02	-0.17 to 0.14	0.01	-0.07 to 0.09	0.28 ^a	0.07 to 0.49
Visual obstruction	1.19 ^a	0.09 to 2.29	1.09	-0.51 to 2.71	-1.15 ^a	-2.07 to -0.23
Annual grass	0.09	-0.01 to 0.21	0.03	-0.06 to 0.11	-0.43 ^a	-0.77 to -0.09
Perennial grass	-0.12	-0.27 to 0.03	-0.14	-0.33 to 0.05	-0.09	-0.28 to 0.11
Residual grass	0.07	-0.29 to 0.44	-0.02	-0.23 to 0.19		
Forb species richness	-0.18	-0.45 to 0.09	-0.04	-0.24 to 0.16		
Forb	0.13 ^a	0.02 to 0.24	-0.06	-0.18 to 0.05		
Variable	Broodless					
	Foraging		Day roost		Night roost	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Sagebrush	-0.08	-0.24 to 0.08	0.03	-0.05 to 0.11	0.04	-0.06 to 0.13
Visual obstruction	1.21	-0.42 to 2.84	0.54	-0.62 to 1.71	-0.25	-1.72 to 1.21
Annual grass	0.01	-0.07 to 0.09	-0.07	-0.14 to 0.01	-0.06	-0.13 to 0.01
Perennial grass	-0.03	-0.14 to 0.08	-0.01	-0.14 to 0.13	0.05	-0.12 to 0.21
Residual grass	0.45	-0.20 to 1.09	0.08	-0.17 to 0.33	0.01	-0.31 to 0.33
Forb species richness	0.09	-0.13 to 0.31	0.00	-0.19 to 0.20		
Forb	-0.00	-0.11 to 0.12	-0.08	-0.17 to 0.02	-0.04	-0.14 to 0.06

^a95% confidence interval does not include zero.

0–2 weeks ($t_{df=29.62} = 5.42$, $P \leq 0.001$). Females with broods 3–5 weeks had a daily range size that was 1.4-times larger ($t_{df=36.98} = 3.71$, $P = 0.002$) and seasonal range size that was 1.7-times larger ($t_{df=30.65} = 4.15$, $P = 0.001$) than females with broods 0–2 weeks. We found females with broods 3–5 weeks did not differ in daily ($t_{df=42.76} = 0.88$, P -value = 0.658) or seasonal ($t_{df=42.37} = 1.43$, P -value = 0.335) range sizes compared with broodless females.

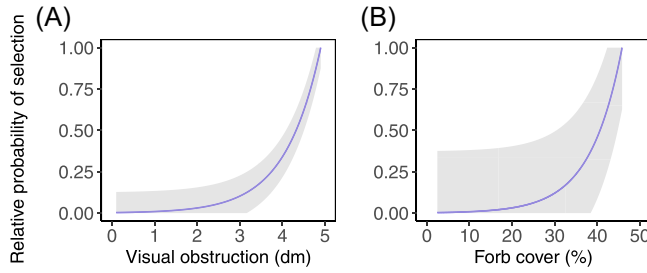


FIGURE 1 Relative probability of selecting visual obstruction (A) and forb cover (B) by greater sage-grouse females with broods 3–5 weeks while foraging. Relative probability of selection was plotted with 95% confidence intervals (shaded areas). Available habitat limits for microhabitat characteristics defines the x-axis limits. Data collected during 2018 and 2019 in Carbon County, Montana, and Park County, Wyoming, USA.

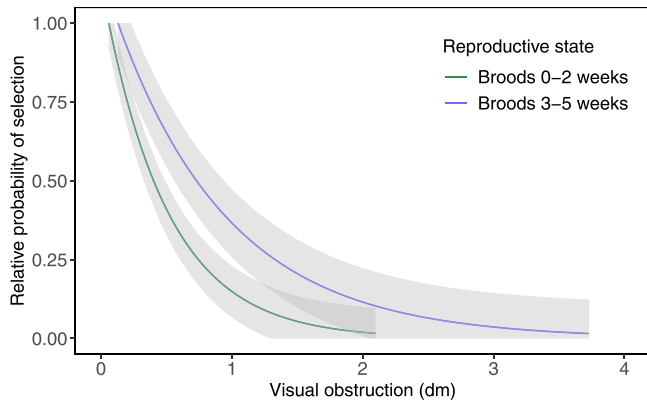


FIGURE 2 Relative probability of selecting visual obstruction by greater sage-grouse females with broods 0–2 weeks and 3–5 weeks while night roosting. Relative probability of selection was plotted with 95% confidence intervals (shaded areas). Available habitat limits for visual obstruction defines the x-axis limit. Data collected during 2018 and 2019 in Carbon County, Montana, and Park County, Wyoming, USA.

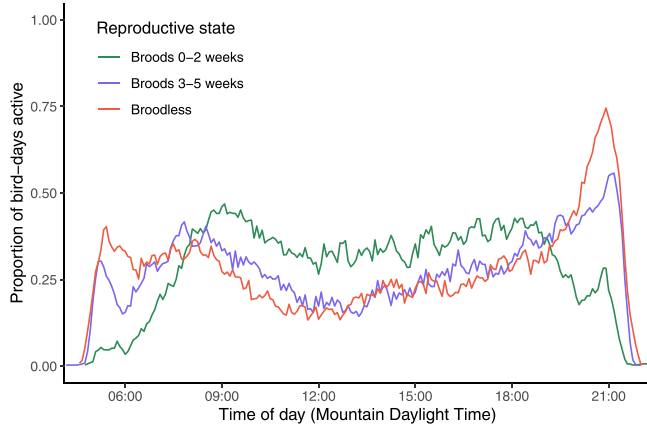


FIGURE 3 Proportion of greater sage-grouse females active during the day for females with broods 0–2 weeks, 3–5 weeks, and broodless females. Activity was defined as the upper 25th quartile of the variance in acceleration (measured every 0.1 sec for 10 sec) along the Z-axis collected at 5-min intervals averaged over a 20-min moving window. Data collected during 2018 and 2019 breeding seasons in Carbon County, Montana and Park County, Wyoming, USA.

TABLE 4 Mean difference, lower and upper confidence intervals (CI), and *P*-values (*P*) from Games-Howell test of mean daily and seasonal range sizes (km²) for female greater sage-grouse (*n* = 66) compared between females with broods 0–2 weeks, broods 3–5 weeks, and broodless females. Data based on mean daily and seasonal range sizes computed as a 95% utilization distribution from a dynamic Brownian Bridge Movement Model for sage-grouse in Carbon County, Montana, and Park County, Wyoming, USA, 2018–2019.

Reproductive state	Daily			Seasonal		
	Difference (km ²)	95% CI	<i>P</i>	Difference (km ²)	95% CI	<i>P</i>
Broods 3–5 wks–Broods 0–2 wks	0.011	0.003 to 0.018	0.002	0.152	0.062 to 0.243	0.001
Broods 0–2 wks–Broodless	–0.007	–0.015 to 0.001	0.021	–0.225	–0.327 to –0.122	0.001
Broods 3–5 wks–Broodless	0.003	–0.005 to 0.011	0.658	–0.072	–0.195 to 0.051	0.335

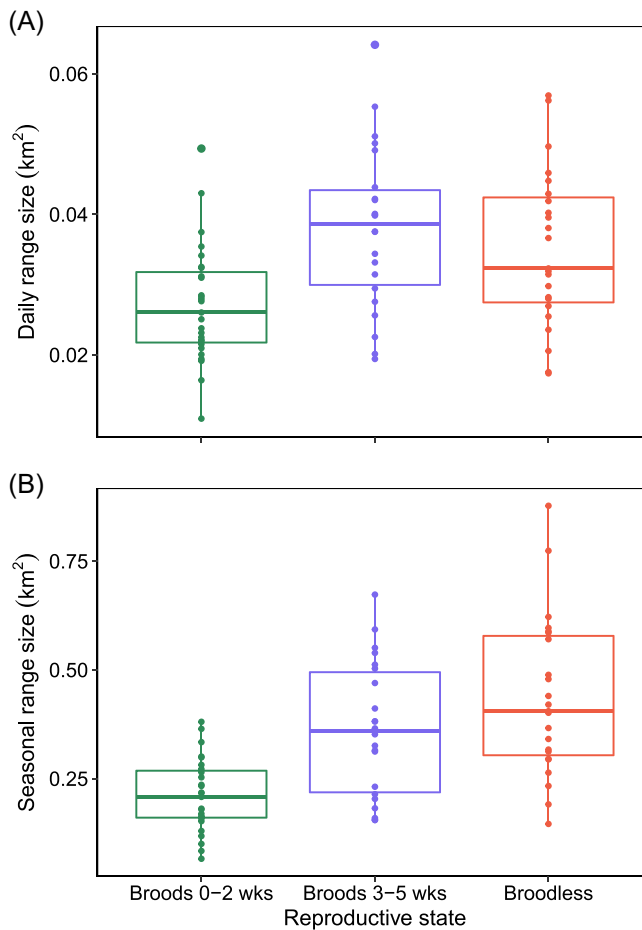


FIGURE 4 Distribution of daily (A) and seasonal (B) range sizes (km²) for females with broods 0–2 weeks (*n* = 27), broods 3–5 weeks (*n* = 22), and broodless females (*n* = 23) computed as a 95% utilization distribution from a dynamic Brownian Bridge Movement Model of greater sage-grouse during 2018 and 2019 breeding seasons in Carbon County, Montana, and Park County, Wyoming, USA. Boxes report the interquartile range (25th–75th percentile) in range size by reproductive state, horizontal lines inside boxes are the median, lower and upper whiskers are 1.5-times the interquartile range, and points above and below whiskers are outliers.

DISCUSSION

The goal of our study was to more comprehensively understand the habitat, and space requirements of female sage-grouse during the breeding season by linking reproductive state, behavioral state, microhabitat selection, daily and seasonal range, and daily activity. We analyzed behavioral and reproductive state influence on microhabitat selection and reproductive state influence on range size and daily activity. We found differences in microhabitat selection based on behavioral state and reproductive state for female sage-grouse. Brood-rearing females selected against visual obstruction at night roosts, while females with broods 3–5 weeks selected for visual obstruction and forbs when foraging, and broodless females showed no selection regardless of behavioral state. Our results confirm previous studies showing differences in habitat selection between brood-rearing and broodless sage-grouse (Gregg et al. 1993, Kirol et al. 2015, Smith et al. 2018). For sage-grouse, incorporating behavioral state aided in understanding differences in daily habitat selection (Roever et al. 2014). Daily and seasonal range size, like in other species, differed by reproductive state with females with young broods having smaller ranges than their counterparts without young (Henry et al. 2005, van Beest et al. 2011, Edwards et al. 2013). Activity levels also differed between reproductive states and changed throughout the course of the day, with a greater proportion of broodless females and females with broods 3–5 weeks being most active in the morning and evening contrasting with a smaller proportion of females with broods 0–2 weeks being active in the morning and evening.

For females with broods 0–2 weeks, we found no significant selection of cover variables when foraging or day roosting, contrary to other studies that have found brood-rearing females selecting for visual obstruction (Mabray and Conover 2015, Schreiber et al. 2015, Smith et al. 2018). Broods 0–2 weeks also showed no selection for forbs, indicating forbs are not significant drivers of habitat selection at the microhabitat scale for younger broods but do become more important for older broods (Smith et al. 2019). Previous research has suggested that when broods are young, female sage-grouse generally select for greater grass cover (Thompson et al. 2006, Hagen et al. 2007), shrub cover (Thompson et al. 2006, Mabray and Conover 2015), and dense sagebrush (Thompson et al. 2006), allowing for protective cover when chicks have limited flight capability. In general, predation has been shown to be the most common cause of yearling/adult sage-grouse mortality (Connelly et al. 2000) and survival of chicks is low during the first week (Gibson et al. 2017). Hence, it has been suggested that brood-rearing females select habitat to maximize both food resources and concealment (Smith et al. 2018), which are positively correlated with chick survival (Gregg and Crawford 2009). Females with broods have also been observed avoiding areas with higher densities of avian predators (Dinkins et al. 2012, Dinkins et al. 2014). However, our results indicated females with broods 0–2 weeks showed no selection for visual obstruction during the day and their probability of selection decreased as visual obstruction increased when night roosting. Our results suggested that females with broods 0–2 weeks have different selection patterns depending on behavior and time of day, and females with broods 0–2 weeks may seek out less cover when night roosting than during the day. We accounted for behavior of brood-rearing sage-grouse in our habitat selection models and compared used sage-grouse locations with random locations that were available to those females (i.e., within an MCP of used locations from the same day) at a smaller scale than most habitat selection studies. Our methods for sampling microhabitat and accounting for behavior may explain discrepancies between our study and others that measure habitat selection on a larger scale that showed females with young broods selected for visual obstruction compared to randomly available habitat (Mabray and Conover 2015, Smith et al. 2018).

Females with broods 0–2 weeks showed different patterns of activity and daily and seasonal range sizes than females with broods 3–5 weeks and broodless sage-grouse. Females with broods 0–2 weeks exhibited smaller daily and seasonal ranges than females with broods 3–5 weeks or broodless females. Smaller daily ranges for younger broods may be due to chicks being brooded by females for about half the day (Schroeder et al. 1999). Sage-grouse broods 0–2 weeks are constrained by the mobility of chicks, and, as chicks age, females are able to increase the size of their ranges (Drut et al. 1994), similar to brood-rearing female dusky grouse (*Dendragapus obscurus*) whose range sizes increased steadily throughout brood-rearing (Sopuck and Zwickel 1992). Females with broods 0–2 weeks were slower to become active in the morning and quicker to lessen activity in the evening compared with females with broods

3–5 weeks and broodless females, similar to activity levels seen in ruffed grouse (*Bonasa umbellus*) broods (Maxson 1974). Less activity in the morning and evening is likely due to females needing to brood their chicks more during cooler temperatures when chicks are still unable to thermoregulate. Females with broods 0–2 weeks then may need to compensate for inactivity by being relatively more active during the day to meet the food requirements of chicks. Predation was related to one-third of sage-grouse chick mortality in Utah (Dahlgren et al. 2010) and the activity pattern of females with broods 0–2 weeks may cause them to be more susceptible to predation.

As chicks became more mobile, females with broods 3–5 weeks showed stronger microhabitat selection than broods 0–2 weeks, possibly in part due to larger daily and seasonal ranges and changes in chick diet. Previous research found that compared with younger broods, selection by older broods for sagebrush cover decreased but forb cover increased, highlighting a shift in habitat selection throughout brood-rearing (Hagen et al. 2007, Smith et al. 2019). Females with broods 3–5 weeks selected for visual obstruction and forb cover when foraging but not when day roosting. Females with broods 3–5 weeks showed variability in selection for shrub cover (Smith et al. 2018), having selected for sagebrush cover when night roosting but made no selection for sagebrush cover while foraging. As broods become older, their rate of survival also increases, and shifts in habitat use might be one reason why chick survival increases as chicks age (Gibson et al. 2017). Females with broods 3–5 weeks selected for forb cover when foraging, but not when day roosting, suggesting females with broods 3–5 weeks were selecting microhabitat relative to behavioral state and their selection changed throughout the day. Forbs are important for brood-rearing sage-grouse (Sveum et al. 1998) and forb cover is selected by broods as they become older (Hagen et al. 2007, Smith et al. 2018, Smith et al. 2019). However, Kirol et al. (2012) found forb cover was not informative for microhabitat selection by broods 3–5 weeks. Differences in microhabitat selection by behavioral state in females with broods 3–5 weeks suggest the need to incorporate behavior in habitat selection studies (Roever et al. 2014). More specifically, habitat studies should focus on times when brood-rearing sage-grouse are exhibiting specific behaviors.

Broodless females were similar to those with broods 3–5 weeks in daily and seasonal range size and activity patterns but differed from females with broods 3–5 weeks in microhabitat selection. Our results indicated broodless females were not strongly selecting for microhabitat features when foraging, day roosting, or night roosting, possibly in part due to broodless females utilizing a greater diversity of cover types (Gregg et al. 1993). Similar to 3–5-week-old brood females, broodless females had larger daily and seasonal ranges than females with broods 0–2 weeks resulting in a greater amount of habitat from which to select. Sveum et al. (1998) and Dunn and Braun (1986) found sage-grouse selected for different habitats in the morning, midday, and afternoon. Activity patterns during the day indicated a greater proportion of broodless females were more active in the morning and evening compared with midday. Broodless females form small, loose flocks and are most active when avian and mammalian predators are also active, which may contribute to their higher survival rate compared with brood-rearing females (Smith et al. 2018). After incorporating behavior, our results suggested broodless sage-grouse utilized a variety of habitats and their selection was not dependent on behavior, even though their activity changed throughout the day.

Foraging animals may allocate time and amount of vigilance differently between different habitat patches to manage predation risk (Brown 1999). Females with young may avoid predation risk more strongly than females without young (Viejou et al. 2018), for example, brood-rearing female black grouse (*Tetrao tetrix*) traded-off food biomass for habitat cover, most likely to reduce predation risk (Signorell et al. 2010). Brood-rearing sage-grouse utilize areas with fewer avian predators, therefore they also select brood-rearing habitat to avoid predators, not necessarily only for microhabitat characteristics (Dinkins et al. 2012, Mabray and Conover 2015). The same habitat may be used between reproductive states but for a different duration of time (Walker et al. 2006, Mackie and Racey 2007). Though we did not directly measure the amount of time sage-grouse spent in different habitat patches when foraging and roosting, we identified that females with broods 0–2 weeks showed different activity patterns than females with broods 3–5 weeks and broodless females.

Combining accelerometer and GPS locations assists researchers in answering questions at the interface of animal behavior and habitat selection (Nathan et al. 2012). Linking habitat selection, range size, and daily activity

provides a comprehensive understanding of habitat and space use by female sage-grouse during the breeding season. Habitat selection, daily and seasonal range size, and daily activity differed across reproductive states, and understanding how these differ will help wildlife managers better accommodate for all individuals in a population. Our results indicated brood-rearing sage-grouse differed in habitat selection by behavior, suggesting broods need a heterogeneous landscape with both forb cover and visual obstruction within their home range to satisfy their daily needs. In addition, a greater proportion of broodless females were active in early morning and late evening compared with brood-rearing females, and therefore many previous habitat selection studies may not have adequately sampled all habitat requirements, especially when broodless females were most likely to be foraging. Quantifying more behaviors and expanding on daily activity (e.g., duration of time spent foraging) should be further examined for sage-grouse and similar species.

MANAGEMENT IMPLICATIONS

Our results highlighted differences in microhabitat selection, daily and seasonal range size, and daily activity between reproductive states, therefore wildlife managers need to account for the variety of habitats and space required by both brood-rearing and broodless sage-grouse composing populations. Microhabitat selection in female sage-grouse differed between day and night, indicating a diversity of habitats is needed to satisfy the requirements for all behavioral states for brood-rearing females. Specifically, our study suggests a reas with more sagebrush cover ($\bar{x} = 18.3\%$, $SE = 1.7$) are needed for night roosts for females with broods 3–5 weeks, a range of visual obstruction ($\bar{x} = 0.9$ dm, $SE = 0.1$) for day and night roosting for brood-rearing females, and areas with greater forb cover ($\bar{x} = 13.7\%$, $SE = 2.4$) for females with broods 3–5 weeks. Broodless females and females with broods 3–5 weeks utilized larger ranges than females with broods 0–2 weeks, therefore conserving large sagebrush landscapes with a diameter between a minimum 0.25–0.50 km, suitable for both reproductive states during brood-rearing is essential to conserving habitat for all female sage-grouse during the breeding season.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

All capture, handling, and post-release monitoring of sage-grouse followed protocols approved by the University of Wyoming Institutional Animal Care and Use Committee (protocols No. 20180102JB00289-01 and No. 20180102JB00289-02) and Montana Fish, Wildlife & Parks Scientific Collector's Permit (No. 2018-072-W and No. 2019-039-W).

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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SUPPORTING INFORMATION

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