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EFFECTS OF LIVESTOCK GRAZING MANAGEMENT ON THE ECOLOGY OF SHARP-
TAILED GROUSE, GRASSLAND BIRDS, AND THEIR PREDATORS IN NORTHERN
MIXED GRASS PRAIRIE HABITATS

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EXECUTIVE SUMMARY

This report summarizes the results of research activities conducted by researchers at Montana State University in 2020 to assess the effects of livestock grazing management and rangeland conditions on the population and spatial ecology of sharp-tailed grouse, grassland birds, and their predators. The primary objectives of this study are to 1) investigate rest-rotation grazing as a rangeland management technique to improve habitat conditions for sharp-tailed grouse and 2) develop a mechanistic understanding of the effects of grazing management on the occurrence and abundance of grassland passerines and mesopredators. Field work concluded in 2019 and a major focus of 2020 was completing analyses and publishing results in peer-reviewed journals.. In this report we present study results for all original project objectives, including those completed during preceding years.

In 2020, we expanded our research objectives to 1) evaluate cumulative effects of livestock grazing management systems on sharp-tailed grouse populations using integrated population models (IPMs), and 2) evaluate habitat selection by sharp-tailed grouse broods in relation to ecological site condition. We report preliminary results for both new objectives.

During 2016–2018, we monitored 95 broods to estimate survival and document habitat use. Twenty-two broods spent the majority of the time (>70% of brood locations) in rest-rotation pastures, 30 spent the majority of time in summer rotation pastures, 29 spent the majority of time in season-long pastures, and 14 split time between multiple grazing systems. Brood success, calculated as the proportion of broods fledging ≥ 1 chick to 14-d of age, was 0.59 ± 0.10 , 0.80 ± 0.07 , 0.66 ± 0.09 , and 0.43 ± 0.13 for broods located on the rest-rotation, summer rotation, season-long and multiple systems, respectively. Of broods that survived to fledging, the proportion of chicks that survived was 0.55 ± 0.08 , 0.54 ± 0.06 , 0.59 ± 0.07 , and 0.32 ± 0.09 for broods located on the rest-rotation, summer rotation, season-long and multiple systems, respectively.

We developed resource selection functions to evaluate hierarchical habitat selection of broods in relation to ecological site descriptions and their relative conditions at two orders of habitat selection. The selection of home ranges of broods was best predicted by the interaction between ecological site type and similarity index, suggesting that the effects of ecological site type were mediated by the relative condition of the site. We found little evidence that ecological site type had any effect on brood habitat selection within a home range. Collectively, our preliminary results indicate that brood-rearing females may prefer certain ecological site types and relative condition when selecting their home ranges. Once home range areas are selected, fine-scale selection of habitats are determined by other, fine-scale habitat conditions.

During 2020, we developed an integrated population model (IPM) to estimate annual rates of finite population changes and evaluate the cumulative effects of livestock grazing management on sharp-tailed grouse populations. This effort yielded estimates of a complete suite of population vital rates, including nest initiation rates of first and reneesting attempts, clutch sizes of first and reneests, hatchability of nests, nest survival of first and reneests, chick survival, juvenile survival, recruitment rates, annual survival of yearlings and adults, as well as finite rates of population growth (λ). Results indicated declining population of sharp-tailed grouse at our study area during 2016–2018, with the largest estimated decrease between 2017 and 2018 ($\lambda = 0.69$; 95%CrI: 0.54–0.84) resulting from depressed fecundity likely due to drought.

During 2020, we published results of this project in three peer-reviewed journals:

- Milligan, M.C., L.I. Berkeley, and L.B. McNew. 2020. Survival of sharp-tailed grouse under variable livestock grazing management. *Journal of Wildlife Management* 84: 1296–1305.
- Milligan, M.C. , L.I. Berkeley, and L.B. McNew. 2020. Habitat use of sharp-tailed grouse in rangelands managed for livestock. *PloSOne* 15(6): e0233756.
- Milligan, M.C., L.I. Berkeley, and L.B. McNew. 2020. Effects of rangeland management on the nesting ecology of sharp-tailed grouse. *Rangeland Ecology and Management* 73:128–137.

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2020 Annual Report

OBJECTIVES

Objective 1: Investigate rest rotation grazing as a rangeland management technique to improve sharp-tailed grouse fecundity and survival.

Accomplishments

Efforts in 2020 focused on completing analyses and publishing results of our field study. Below we report complete results for the entire 4-year study.

Methods:

Fecundity.—Sharp-tailed grouse were trapped at 12 leks (5 in rest-rotation pastures, 3 in summer rotation pastures, and 4 in season-long pastures) using walk-in funnel traps during March-May, 2016-2018. We recorded standard morphometrics including body mass, wing chord, tarsus length, and culmen length, and fitted all birds with a uniquely numbered metal leg band. Birds were sexed and aged by plumage characteristics. Males were fitted with a unique combination of color bands to allow for resighting at leks next year. We fit captured females with 18-g necklace-style radio-transmitters with a 6-8 hour mortality switch and an expected battery life of 12 months (model A4050; Advanced Telemetry Systems, Insanti, MN). Previous work found no impact of necklace-style radio-transmitters on prairie-grouse demography (Hagen et al. 2006). All animal handling was approved under Montana State University's Institutional Animal Care and Use Committee (Protocol #2016-01).

Radio-marked females were located by triangulation or homing ≥ 3 times/week using portable radio receivers and handheld Yagi antennas during the nesting and brood-rearing period (April—August). When females localized in an area and their estimated location did not change for 2 successive visits, we assumed that the female was sitting on a nest. For half of the females, we used portable radio receivers and handheld Yagi antennas to locate and flush the female so eggs could be counted and the nest location recorded with a handheld GPS unit. We marked nest locations with natural landmarks at a distance ≥ 25 m to aid in relocation. Nest sites were not visited again until it was determined that the female had departed (i.e., was located away from the nest for ≥ 2 days during incubation and ≥ 1 day after expected hatch date) due to successful hatching of the clutch or failure due to either predation or abandonment. Nesting females were otherwise monitored by triangulation from a distance > 25 m. Thus, nest sites for half of the females were only disturbed by the presence of an observer a maximum of 1 time during the laying and incubation period. The remaining half of the females were never flushed and nest attempts were monitored from a distance of > 25 m to evaluate whether the protocol of flushing females has a negative effect on nest survival. A female was assumed to be incubating if she was located in the same location for 2 consecutive visits and nest sites were only visited after the female was located away from the nest for ≥ 2 days during incubation or ≥ 1 day after expected hatch date.

Once the female departed the nest, we classified nest fate as successful (≥ 1 chick produced), failed, depredated, or abandoned. Nests were considered abandoned if eggs were cold and unattended for > 5 days. Nests were considered failed if the eggs were destroyed by flooding,

trampling by livestock, or construction equipment. Nests were considered depredated if the entire clutch disappeared before the expected date of hatching, or if eggshell and nest remains indicated that the eggs were destroyed by a predator. When a predation event occurred, the egg remains were evaluated and the area was searched for predator sign. For successful nests, hatchability was calculated as the proportion of the total clutch that hatched and produced chicks. Eggs that failed to hatch were opened to determine stage of development and possible timing of embryo failure.

Successful broods were relocated ≥ 3 times/week until failure. Pre-fledging brood survival was estimated by conducting flush counts between 14 and 16 days post hatch. Fledging was considered to occur at 14 days post hatch because at that point chicks are able to thermoregulate and are capable of weak flights (Pitman et al. 2006). Flush counts were conducted at dawn when chicks were close to radio-marked females to determine the number of surviving chicks in the brood. After females were flushed, the area was systematically searched and the behavior of the female observed to assess whether chicks were present but undetected. For counts of 0 chicks, the brood female was flushed again the following day to be certain no chicks remained in the brood. Broods were considered successful if ≥ 1 chick survived until fledging at 14-d post-hatch (Pitman et al. 2006). Flush counts were repeated at 14, 30, 45, and 60 days post-hatch or until we were confident that no chicks remained with the female.

We monitored radio-marked females ≥ 3 times per week to estimate survival. Transmitters were equipped with a mortality switch that activated after 6–8 hours of inactivity. Once the mortality switch activated, transmitters were located and the area searched to determine probable cause of death. Mortality events were classified as either predation, hunter, other, or unknown. Predation mortalities were further identified as either mammal, avian, or unknown predator. A mortality event was classified as mammalian predation if bite marks, chewed feathers, or mammalian tracks were present. Mortality was determined to be avian predation if the carcass had been decapitated and/or cleaned of the breast muscle with no bite marks, or if the feathers had been plucked. If there were conflicting signs of mortality, the event was classified as unknown predation. Females were censored from the study if their collars were found with no sign of death or if they could not be located for ≥ 2 months.

We evaluated habitat conditions at each nest and brood flush site within 3 days of hatching or expected hatch date in the case of failure. We recorded visual obstruction readings (VOR) at the nest bowl and at four points 6 m from the nest in each cardinal direction. At each point, VOR was measured in each cardinal direction from a distance of 2 m and a height of 0.5 m using a Robel pole (Robel et al. 1970). We estimated non-overlapping vegetation cover (percent new grass, residual grass, forbs, shrubs, bare ground, and litter) at 12 subsampling locations within 6 m of the nest using a 20×50 cm sampling frame (Daubenmire 1959). At each subsampling plot, we measured the heights of new grass, residual grass, forbs, and shrubs. We also estimated shrub cover using the line-intercept method, recording the species, height, and length of each shrub intersecting the transect. For nests, we conducted parallel sampling at randomly selected points within a study area defined by a minimum convex polygon placed around the leks of capture and buffered to 2 km. For broods, we conducted parallel sampling at paired points in a randomly determined direction and distance (maximum of 250 m) from each flush location to represent available habitat within the average daily distance traveled by broods (Goddard et al. 2009). Random points that fell within unsuitable habitat (i.e., water, cultivation) or were located on properties to which we did not have access were replaced.

We also measured habitat conditions at the home range scale (500 ha, based on estimated home range sizes of sharp-tailed grouse during the breeding season, see below) under the assumption that the home range contained the resources utilized by a female during the nesting season. The home range area was defined as a circular plot with a 1,300-m radius centered on each nest, brood, and random location. We calculated habitat variables at the home range scale using remotely sensed data and ArcMap 10.4. We included road datasets for both Montana and North Dakota and calculated the distance to paved and gravel roads from the nest bowl (Montana State Library, North Dakota GIS Hub Data Portal). Paved roads, including state highways, had higher traffic volumes and were assumed to represent a different level of disturbance than gravel roads. We also included the locations of oil pads which represented another form of disturbance in the study area and calculated the distance to the nearest oil pad from the center of each home range. Landcover analyses utilized the 30 m resolution LANDFIRE data depicting vegetation type (LANDFIRE 2013). We measured the distance from the center of each home range to the nearest patch of non-grassland habitat. In addition, we used the Patch Analyst Extension in ArcMap to calculate the proportion of grassland, the density of edge habitat, and grassland shape complexity.

We collected stocking information from cattle producers for every pasture in which radio-marked sharp-tailed grouse were located. For each pasture, we recorded the type of animal (cow/calf pairs, heifers, bulls, or horses), number of head, and the dates when animals were in the pasture. We calculated the following grazing management variables: grazing system (rest-rotation, summer rotation, season-long), stocking rate (AUM ha⁻¹), stocking intensity (AU ha⁻¹), stocking duration (in months), and season of stocking (growing season [May—July], post-growing season [August—November], winter [December—April], or rest [no grazing for entire year]).

We used field data to estimate eight demographic parameters related to fecundity for sharp-tailed grouse (Table 1). Some of these parameters, including clutch sizes and chicks per egg laid (CPE), can be estimated directly from field data. However, other parameters are observed imperfectly. Nests are not observed from the initiation date and nests that fail before discovery must be considered to make population-level inferences. To account for imperfect observation, we used the nest survival model in Program MARK to calculate maximum likelihood estimates of daily nest survival (NSURV) following the methods described below.

Nesting rate (NEST) was calculated as the percentage of females that attempted a nest. The probability of reneating (RENEST) was calculated as the number of observed reneating attempts divided by the number of unsuccessful first nests minus the number of females that had first nests but were unavailable to reneate. A hen was considered unavailable if she was killed during the first nest attempt or was not relocated after the failure of a first nest attempt. Initial brood size was determined by the number of chicks that were known to hatch based on nest observations. Brood success (BSURV) was calculated as the proportion of broods that successfully fledged ≥ 1 chick. Fledging success (FPC) was calculated as the proportion of chicks that survived until fledging among successful broods. Broods were included in the easement category if $>70\%$ of brood locations were within the easement boundaries, in the reference category if $>70\%$ of locations were in the reference area, and in the category “both” if they split their time between the two areas.

Fecundity (F), or the number of female fledglings produced per female, is expressed as a function of these parameters using the following equation:

$$F = [(NEST * CS_1 * NSURV_1) + [(1 - NSURV_1) * RENEST * CS_2 * NSURV_2]] * CPE * BSURV * FPC * 0.5$$

Bootstrapping procedures were used to calculate 85% confidence intervals for fecundity estimates by randomly drawing from the underlying distributions of input parameters (McNew et al. 2012).

Nest success is defined as the probability of a nest producing ≥ 1 chick, whereas nest survival accounts for potential losses of nests before discovery. We constructed nest survival models using the RMARK package in Program R to calculate maximum likelihood estimates of daily nest survival and evaluate the effects of habitat conditions and management variables on daily nest survival during a 77-d nesting period during 28 April – 12 July (White and Burnham 1999, Dinsmore et al. 2002). Before fitting models, we examined correlations for each pair of variables and if a pair was highly correlated ($r \geq 0.5$, $p < 0.05$), we used single-factor models to determine which of the two variables accounted for the largest proportion of variation in daily nest survival. We considered the variable with the lowest model deviance to be the primary variable to consider in subsequent analyses.

We evaluated nest survival models at both the habitat and management level and compared model sets using the criteria described above. For the habitat-level analysis, underlying effects included variables of nest attempt, female age, female condition, flushing effect, daily temperature, and three precipitation variables compared to a null model of constant daily nest survival (Goddard and Dawson 2009). Female condition was calculated by regressing body mass against the length of the wing chord using the reduced major axis method (Green 2001). Precipitation variables included daily precipitation with a 1-day time lag, growing season precipitation from the previous year (total precipitation from previous April to June), and available precipitation from that year (total precipitation from October to May). We then selected the most parsimonious models at each of the different spatial scales (nest- and home range level) and assessed them in the final candidate model set. The management-level analysis included all the models evaluated in the nest site selection analysis (described above), plus a model examining the effect of stocking density while the nest was active. Top variables from both the habitat- and management-level analyses were then combined in a final candidate model set to evaluate relative effects on nest survival.

We also developed a separate set of candidate models to examine the effects of grazing variables on nests within the rest-rotation pastures ($n=57$) and evaluate effects on nest survival of the different treatments within the system (grazed during the growing season, grazed post-growing season, rested entire year).

Overall nest survival for precocial species is the probability that a nest will survive the entire nesting period, defined as the mean laying plus incubation interval for grouse at our study sites (37-d). We calculated the overall nest survival probability with parametric bootstrapping, using the beta estimates and variance-covariance matrix from the top model in the nest survival analysis. Variance of overall nest survival was estimated with the delta approximation (Powell 2007). The average duration of incubation period (27-d) was determined from observations of our sample of successful nests and from previous work (Connelly et al. 1998).

Survival.— We calculated cumulative breeding season survival of radio-marked females using staggered entry Kaplan-Meier models with package survival in Program R (version 3.5.1, R Foundation for Statistical Computing, Vienna, Austria). We created weekly encounter histories

for each female for the 5-month period from 15 March to 15 August and encounter histories included the week of entry, week of exit, and event (0 = survived, 1 = mortality). We excluded females that died within a week of capture ($n = 6$) to account for any bias that might be due to capture stress. Data were both left- and right-censored to account for the staggered entry of birds into the sample and the loss of birds that left the study area ($n = 9$). Some females were monitored in multiple years, so we modeled individual identity as a random effect using the ‘cluster’ function. We first tested whether the assumption of proportional hazards was met and then included an interaction with time for covariates for which the assumption was not met (Fox 2002). We used Cox proportional hazards models to evaluate differences in breeding season survival among years, female age (second-year vs. after second-year), and grazing system (rest-rotation, summer rotation, season-long). For females with ≥ 30 locations (Seaman et al. 1999), we calculated the proportion of each grazing system within a female’s 50% kernel home range and assigned a grazing system based on the system containing $\geq 60\%$ of the home range. To calculate 50% home ranges, we used the fixed kernel method (Worton 1989) with the default smoothing parameter using the `adehabitatHR` package in Program R. For females with < 30 locations (28% of monitored females), we assigned a grazing system based on the system with the majority ($\geq 60\%$) of that individual’s locations. Females for which one grazing system did not account for $\geq 60\%$ of either the 50% kernel home range or locations were excluded from analyses.

We calculated cumulative survival rates of radio-marked females for the 7-month non-breeding season separately using staggered entry Kaplan-Meier models with monthly encounter histories for each female for the period from September through March. We used the ‘cluster’ function to model individual identity as a random effect to account for females monitored in multiple years. Similar to analyses of breeding season survival, we used Cox proportional hazards models to evaluate differences in non-breeding season survival among years and female age (second-year vs. after second-year). Data for the non-breeding season was collected on a monthly basis, which precluded analyses evaluating differences in non-breeding season survival among grazing system. We used estimates of survival during the breeding and non-breeding seasons to calculate annual survival and variance of overall survival was estimated with the delta approximation method (Seber 1982).

For both breeding and non-breeding season survival, we compared models using Akaike’s Information Criterion adjusted for small sample sizes (AICc) and model selection was based on both minimization of AICc and AICc weights (w_i ; Burnham and Anderson 2002). Parameters were considered uninformative if $\Delta\text{AICc} < 2.0$ for models that differed by a single parameter or if 85% confidence intervals overlapped 1 for hazard ratios (Arnold 2010). The effects of year, female age, and grazing system are reported as hazard ratios (HR, $e\beta$), where the ratio equals 1 if there is no difference in the risk of mortality among strata.

We calculated hazard functions to evaluate seasonal patterns of mortality. We used the smoothing splines functions in package `gss` in Program R to calculate hazard functions based on weekly survival data (DelGiudice et al. 2006). Hazard functions assess the instantaneous risk of mortality in each week given that an individual had survived to that point. To avoid overfitting splines, we used the default value for the smoothing parameter. We calculated separate hazard functions for females in each of the three grazing systems to evaluate the effects of grazing management on seasonal patterns of mortality risk.

We used Andersen-Gill models for survival to model the effects of habitat selection on mortality risk during the breeding season (Andersen and Gill 1982). For these models, we formulated another set of encounter histories for each female for the 5-month breeding season (15 March–15 August). Each encounter history is structured so that the entry represents the interval between successive relocations of an individual and individual females have multiple encounter histories in the dataset. Encounter histories included the day of entry, day of exit, length of the interval, the animal's fate at the end of the monitoring interval (0 = right-censored, 1 = mortality), and the covariates representing habitat features associated with each relocation event as measured at the end of the interval (Johnson et al. 2004). Mortality events were likely to occur at the end of the interval and previous studies found no bias regarding when habitat features were measured within a relocation interval (Johnson et al. 2004). We fit the Andersen-Gill formation of the Cox proportional hazards model using the 'coxph' function in package survival in Program R and evaluated the spatial variation in risk factors for females relative to time-varying individual features, landcover, anthropogenic disturbance and rangeland management. Before fitting models, we examined correlations for each pair of explanatory variables ($r \geq 0.5$; Supporting Information). We then used the 'cox.zph' function to test the assumption that hazards vary linearly across predictor variables (Fox 2002).

We first examined single-variable models with habitat and individual time-varying covariates predicted a priori to affect grouse mortality risk. We evaluated mortality risk relative to time-varying individual features, weather, anthropogenic disturbance, and landcover. Individual features included categorical variables representing whether a female had either an active nest or a brood. We obtained daily precipitation data from the National Oceanic and Atmospheric Association (NOAA) station in Sidney, MT, and calculated the total amount of precipitation during each monitoring interval to capture variation in environmental conditions. We digitized the locations of oil pads and roads, both forms of anthropogenic disturbance in our study area, and calculated the distance to the nearest oil pad or road from each point. Landcover analyses utilized the 30-m resolution LANDFIRE data depicting vegetation type (LANDFIRE 2013). We used the Patch Analyst Extension in ArcMap to calculate the density of edge habitat (total landcover edge length / polygon area) and the amount of cropland within a range of buffer distances (30, 75, 125, 200, 500, 750, 1000, 1300 m). A habitat patch edge was defined as an abrupt change between any of the three main habitat types (grassland, wooded draws, and cropland) and edge density was defined as the amount of patch edge relative to the area within a given buffer distance. In our study area, cropland consisted primarily of dryland wheat. We used an information-theoretic approach to first choose the spatial scale that best represented the relationship between mortality risk and each habitat variable.

Our final candidate model set included 24 models that estimated the additive effects of 3 grazing management variables in combination with the important habitat and individual covariates based on preliminary analyses. Rangeland management variables included grazing system and stocking rate (AUM ha⁻¹) during both the current and previous year. We compared Andersen-Gill models using AICc and based model selection on both the minimization of AICc ($\Delta AICc < 2$ from best-fit model) and AICc weights ($\sum w_i > 0.3$). Models that differed from the top model by a single parameter with $\Delta AICc < 2.0$ or whose 85% confidence intervals overlapped zero were considered uninformative (Arnold 2010).

Results

Mean overall lek attendance was 11.7 birds (average of 9.5 males and 2.2 females) during the study period. Lek attendance declined at all but one lek in 2018, with overall attendance at individual leks declining 33-57% compared to previous years, with the most marked declines occurring in male attendance. Female attendance occurred significantly later than in previous years, with the first female observed on 10 April, which was about 2 and 3 weeks later than in 2017 and 2016, respectively. Female attendance also peaked later in the year, with the majority visiting between 24 and 27 April.

We captured a total of 757 sharp-tailed grouse at leks during 2016–18, including 431 individuals (211 females, 220 males; Table 2). We fitted 174 females (102 yearlings, 72 adults) with radio-transmitters.

Fecundity.— We located 188 grouse nests in treatment pastures (147 first nests, 41 re-nesting attempts) laid by 128 individual females during 2016–2018 (Fig. 1). Nesting frequency (\pm SE) was 1.00, while the probability of re-nesting after first nest failure was 0.61 ± 0.10 . Hatch rate of eggs (\pm SE) was $91.3 \pm 2.4\%$. Mean clutch size for all nest attempts was 10.2 ± 0.59 eggs. Mean clutch size for first nest and re-nests was 11.1 ± 0.57 and 9.6 ± 0.60 eggs, respectively.

Overall nest survival varied by year and ranged from 0.29 ± 0.06 in 2016 to 0.48 ± 0.07 in 2018. Preliminary analyses suggested that visual obstruction averaged across the 6-m radius plot best predicted daily nest survival and that a pseudo-threshold model best represented the relationship between visual obstruction and nest survival, so only models with the natural log transformation of average VOR were included in analyses (see Appendix C; Milligan 2019). At the nest-level, VOR was in the top four models, accounting for 91% of the relative support of the data. Percentage forb, residual grass, and new grass in combination with VOR each received some support (Δ AICc = 0.50 – 1.83, w_i = 0.13 – 0.26) and so were examined in the final model set. At the home-range level, distance to road received the most support (Δ AICc = 0, w_i = 0.35) and proportion grassland marginally improved model fit compared to the null model (Δ AICc = 1.36, w_i = 0.18), so both variables were included in the final analysis. In the final candidate model set, the model that included VOR, percentage forbs and proportion grassland received the most support (Δ AICc = 0, w_i = 0.43, Table 3). VOR was in all twelve top models, accounting for 100% of the relative support of the data, while proportion grassland accounted for 79% of relative support. Confidence intervals for VOR, proportion grassland, and distance to road did not overlap zero, indicating significant effects (Fig. 2). Daily nest survival increased with proportion grassland (β = 0.16 ± 0.10), distance to road (β = 0.21 ± 0.11), and VOR up to a threshold of 20–30 cm, as represented by the pseudo-threshold model (β = 0.29 ± 0.11).

In the management-level analysis, stocking density while the nest was active was the best predictor of daily nest survival, accounting for 66% of the relative support of the data (Table 3), with survival increasing with stocking density (β = 0.30 ± 0.14 , Fig. 3). Confidence intervals for stocking rate in both the current and previous year overlapped zero (stocking rate in cur. yr: -0.17–0.06; stocking rate in prv. yr: -0.18–0.25), but there was also evidence for an effect of year and rest-rotation grazing, with confidence intervals that did not overlap zero. Daily nest survival was higher in both 2017 (β = 0.36 ± 0.25) and 2018 (β = 0.73 ± 0.28) than in 2016 and was lower in rest-rotation pastures compared to season-long pastures (β = -0.44 ± 0.27). Overall nest survival (\pm SE) was 0.48 ± 0.07 in season-long pastures, 0.38 ± 0.06 in summer rotation pastures, and 0.32 ± 0.06 in rest-rotation pastures (Fig. 4). In the full analysis, the model with the most support included VOR, proportion grassland and stocking density while the nest was active

($\Delta AICc = 0$, $w_i = 0.90$, Table 3), with confidence intervals for all three variables not overlapping zero, suggesting significant effects.

For nests within the rest-rotation system ($n=57$), there was no evidence for an effect of the timing of grazing (grazed during the growing season, grazed post-growing season, or rested entire year) on nest survival (Table 4). Estimates of overall nest survival in the three treatments overlapped entirely (Fig. 4).

We monitored 95 broods to estimate survival and document habitat use (Table 5). Twenty-two broods spent the majority of the time ($>60\%$ of brood locations) in rest-rotation pastures, 30 spent the majority of time in summer rotation pastures, 29 spent the majority of time in season-long pastures, and 14 split time between multiple grazing systems. Brood success, calculated as the proportion of broods fledging ≥ 1 chick to 14-d of age, was 0.59 ± 0.10 , 0.80 ± 0.07 , 0.66 ± 0.09 , and 0.43 ± 0.13 for broods located on the rest-rotation, summer rotation, season-long and multiple systems, respectively. Of broods that survived to fledging, the proportion of chicks that survived was 0.55 ± 0.08 , 0.54 ± 0.06 , 0.59 ± 0.07 , and 0.32 ± 0.09 for broods located on the rest-rotation, summer rotation, season-long and multiple systems, respectively.

We determined that 28 females were killed by predators: 15 and 8 by mammalian and avian predators, respectively, and 5 by an unknown predator. An additional 2 females were hunter mortalities. One female was right censored from the study when the transmitters was found with no sign of death. An additional 4 females left the study area within 2 weeks of captured and were right censored after they could not be relocated for more than 2 months. Two females moved onto land to which we do not have access and so were monitored solely for survival.

Eight demographic parameters were estimated using field data (Table 6). Estimated fecundity, the number of female fledglings produced per female per year, was 1.14 (95% CI = 0.82 – 1.53) female fledglings produced per female.

Survival.— We evaluated survival for 153 female sharp-tailed grouse, some of which were monitored in multiple years, resulting in 180 bird-years (2016: $n = 55$, 2017: $n = 64$, 2018: $n = 61$). Of the 180 bird-years, 66 represented females primarily using the rest-rotation system, 60 using the summer rotation system, 46 using the season-long system, and 8 splitting time among multiple grazing systems. Overall, 86% of mortality events were due to predation, with the remaining mortality events due to hunter harvest (8%) or unknown causes (6%).

The assumption of proportional hazards for breeding season survival was not met for either year or grazing system, so models that included those variables also incorporated an interaction with time. Overall survival (\pm SE) during the 5-month breeding season for female sharp-tailed grouse across all years and grazing systems was 0.65 ± 0.04 , which corresponds to a monthly survival rate of 0.91 ± 0.005 . Despite significant annual variation in precipitation, breeding season survival did not differ significantly among the 3 years of study (baseline: 2016; Cox proportional HR for 2017 = 0.72, 95% CI = 0.07–7.02, $Z = -0.29$, $P = 0.78$; Cox proportional hazards HR for 2018 = 5.7, 95% CI = 0.52–63.74, $Z = 1.42$, $P = 0.16$). There was also no difference in breeding season survival between female age classes (baseline: second-year; Cox proportional hazards HR = 1.19, 95% CI = 0.72–1.96, $Z = 0.69$, $P = 0.49$), or among grazing systems (baseline: season-long; Cox proportional hazards HR for summer-rotation = 1.13, 95% CI = 0.15–8.82, $Z = 0.12$, $P = 0.90$; Cox proportional hazards HR for rest-rotation = 1.49, 95% CI = 0.17–13.29, $Z = 0.36$, $P = 0.73$). Although there was weak evidence for an effect of age and year on survival (Table 7), confidence intervals for both age groups (second-year: 0.524–0.735, after second-year: 0.558–

0.757) and all 3 years (2016: 0.540-0.793, 2017: 0.540-0.778, 2018: 0.545-0.785) entirely overlapped. Breeding season survival was similar across grazing systems (Fig. 5).

In contrast, non-breeding season survival differed among the 3 study years (Table 7; baseline: 2016; Cox proportional HR for 2017 = 2.93, 95% CI = 1.30–6.58, $Z = 2.59$, $P = 0.009$; Cox proportional hazards HR for 2018 = 1.38, 95% CI = 0.52–3.67, $Z = 0.65$, $P = 0.52$), with non-breeding survival in 2017 significantly lower than in either 2016 or 2018. Overall survival during the 7-month non-breeding season was 0.78 ± 0.07 in 2016, 0.43 ± 0.08 in 2017, and 0.71 ± 0.08 in 2018, with monthly survival rates of 0.97 ± 0.007 , 0.89 ± 0.005 , and 0.95 ± 0.008 in 2016, 2017, and 2018, respectively. Annual survival for the population was 0.50 ± 0.05 in 2016, 0.28 ± 0.04 in 2017, and 0.46 ± 0.05 in 2018.

We calculated hazard functions for females that used the rest-rotation, summer rotation, and season-long systems to evaluate potential differences in seasonal patterns of mortality risk among the different grazing systems. Mortality risk peaked in early May during the nesting period in all grazing systems, but seasonal patterns differed across grazing systems (Fig. 6), although error estimates were large so differences should be treated with caution. The increase in mortality risk during the nesting period was greatest in the rest-rotation system, with a 61–82% higher risk of mortality in the rest-rotation compared to season-long and summer rotation systems, respectively (Fig. 6). However, there was an additional peak in mortality in both season-long and summer rotation systems in late summer that did not occur in the rest-rotation system, with the risk of mortality 3–4 times higher in the season-long and summer rotation systems, respectively, compared to the rest-rotation system (Fig. 6). The difference in peaks of mortality risk among systems translated to no effect of grazing system on cumulative survival calculated for the entire breeding season (Fig. 5).

To evaluate the spatial covariates influencing mortality risk during the breeding season using Andersen-Gill models, we pooled females from all years and age-classes, which included data from 164 females across 192 bird-years, encompassing 6,783 locations, and included locations from individuals that were not monitored for the entire breeding season and so were not used in the previous analyses. The assumption of proportional hazards was met for a global model including all covariates. Preliminary analyses suggested that the edge density within 75 m and the proportion cropland within 1,300 m best predicted mortality risk (Milligan 2019). Of the single-variable preliminary models, edge density within 75 m, the proportion cropland within 1,300 m, and whether a female had an active brood all improved model performance compared to the null model and so were included in the full candidate model set with grazing management variables. There was no evidence for an effect of anthropogenic disturbance, including either oil pads or roads. In the full model set, the top model contained the effect of cropland within 1,300 m, which accounted for 49% of the relative support of the data across all models (Table 8). The risk score increased with the amount of cropland within 1,300 m of a bird's location ($\beta = 0.02 \pm 0.02$; Fig. 7). However, there was considerable model uncertainty and the model containing the effect of cropland represented only a modest improvement over the null model (Table 8). Effects relative to livestock grazing management were not supported (Table 8).

Objective 1a: Evaluate cumulative effects of livestock grazing management systems on sharp-tailed grouse populations using integrated population models (IPMs)

Methods:

Integrated Population Models—The Bayesian framework is particularly useful in the field of ecology for combining multiple, sometimes dissimilar sources of data and estimating parameters of complex data sets (Kéry and Shaub 2012). In addition, Bayesian methods allow explicit modeling of both the ecological (or state) process and the observation process, which is critical when models are used to inform management decisions. Thus, we used a Bayesian hierarchical framework to develop an integrated population model (IPM) that combines multiple independent sources of population data including spring lek counts and a female-based stochastic population model with two stage classes (yearlings and adults). Our methodology is similar to IPMs developed previously for greater sage-grouse (Coates et al. 2018) and informed by procedures described in Kéry and Shaub (2012) and Halstead et al. (2012). An advantage of IPMs over population models developed only with demographic data is the estimation of latent population parameters that were not directly measured; estimation of derived parameters provide a more thorough understanding of population dynamics between and within stage classes, years, and sites (Schaub and Abadi 2011). We were chiefly interested in evaluating whether grazing system (summer rotation, rest-rotation, or season-long) differentially influenced vital rates and population growth rates of sharp-tailed grouse in western MT and eastern North Dakota.

Population Count Data—According to Abadi and Schaub (2011), “IPMs represent the single, unified analysis of population count data and demographic data.” The foundation of IPMs is population count data. For 12 surveyed leks from 2016 through 2018, we compiled three repeated lek counts during a short 5-day window each year (to address the assumption of population closure) along with counts of the maximum number of males per lek. Maximum and repeated counts were entered into a single season N -mixture model to adjust for systematic downward bias in the observation data (Royle 2004). The N -mixture model was specified as:

State Process:

$$N_{l,y} \sim \text{Poisson}(\lambda_y)$$

$$\text{Log}(\lambda_y) = \alpha_0$$

Observation Process:

$$C_{l,y,r} | N_{l,y} \sim \text{Binomial}(N_{l,y}, P_y)$$

$$\text{Logit}(P_y) = \beta_{0,y},$$

where subscripts l , y , and r denote the specified lek, year, and repeated counts respectively. The state process equations model the latent unobservable number of males associated with each lek (local abundance), and the observation process equations model the variation among repeated counts within a year at each lek and estimate the probability of detecting a grouse. Although most birds counted on the leks are males, we assume a 1:1 sex-ratio and therefore used the male counts as a proxy for the number of females in the population, which are much more difficult to count.

Survival and reproductive data comprise the second major component of our IPM: the demographic data and sub-component models. The life-histories of grouse are often represented by a two stage-class conceptual diagram where the nodes represent stage-classes (yearlings = females 10 – 20 months of age, adults = females > 20 months of age) and arrows represent major population vital rates (Hagen et al. 2009, McNew et al. 2012, Coates et al. 2014). This

conceptual model is then transformed into a 2-stage stochastic Lefkovich population matrix for subsequent analyses (Caswell 2001).

Survival—We modeled annual survival for both stage classes of female STGR monitored via radio-telemetry, survival of first and second nests, and survival of chicks from hatch until 35 days old as continuous processes observed at discrete intervals. For each discrete monthly interval, adult birds were classified as dead, alive, or censored. We constructed histories of nests and chicks using days as time intervals (Halstead et al. 2012). Using a constant hazard model, we assumed the probability of mortality was equal across the length of the study and assumed that risk of mortality was independent among individuals. Left censoring occurred prior to individuals entering the study (time of capture and initiation of laying for nests) allowing for staggered entry common to radio-telemetry and reproductive ecology studies. Right censoring occurred after mortality, loss of radio, and for birds still alive at the end of the study period (after year 2018), meaning that all individuals had a recorded mortality event or were eventually right-censored. Following modeling procedures described in Halstead et al. (2012), the survival function for the constant hazard model was estimated as:

$$S_{ijl} = e^{-CH_{ijl}}, \text{ where } CH_{ijl} = \sum_{j=1}^T UH_{1;j,il} \text{ and}$$

$$UH_{ijl} = \exp(\gamma_0 + \beta_{age,ij} * x_{age,ij} + \kappa_{ij} + \beta_{grz1} * x_{grz1} + \beta_{grz2} * x_{grz2})$$

Subscript i references individual grouse, nests, or chicks and subscripts j and l reference units of time and survival year respectively. T is the last time interval in the monitoring period. Symbol γ_0 is the mean baseline hazard and models for adult survival, first and second nest survival, and chick survival included random effects for individual hen age ($\beta_{age,ij}$, where the indicator was equal to one for yearlings) and year (κ_{ij}) to account for individual and annual variation. Parameters β_{grz1} and β_{grz2} are the magnitude of the expected change in the $\ln(\text{hazard ratio})$ depending on grazing system type, where season-long is the reference category and indicator variables specify rest-rotation (x_{grz1} equal to one) and summer rotation (x_{grz2} equal to one) systems. Hazard ratios measure an effect on an outcome of interest over time, in this case the effect of grazing system on grouse survival. The hazard represents the instantaneous event rate. The hazard ratio is interpreted as the relative likelihood a particular group will experience the event of interest compared to the reference group. Thus, if the hazard ratio is less than one, the treatment group is less likely than the reference group to experience the event of interest (i.e., a hazard ratio of 0.5 would mean that a female grouse in that grazing system is half as likely to experience mortality at a particular point in time compared to a grouse in the reference grazing system, season-long). A hazard ratio equal to one implies no difference in treatment from the reference group, and therefore, if the 95% credible interval includes one, we do not have evidence of a difference in probability of survival between the treatment group and the reference group.

To classify grazing system for models of adult survival, we simply used the classification with the highest recorded frequency of locations during the time period of interest (e.g., if a hen was located in season-long pastures ten times and rest-rotation five times, the grazing system was classified as season-long for that hen in the adult survival model). For first and second nests, we simply used the grazing system in which each nest was located. We used uninformative priors for all parameters.

Fecundity—Fecundity was defined by several sub-models, each of which specifically estimated important reproductive vital rates for STGR. Parameters estimated by individual stochastic sub-models included nest propensity (np ; first nest = $np1$ and second nest = $np2$), nest survival (ns ; described above), clutch size (cl), egg hatchability (h), chick survival (cs ; described above), and juvenile survival (js). We did not monitor juvenile grouse after 35 days of age. One of the advantages of IPMs is the estimation of vital rates for which no data were collected (Kéry and Schaub 2012). Therefore, we used an informative prior in our sub-model of juvenile survival (js) based on published rates in the literature for greater sage-grouse and prairie-chickens (Pitman et al. 2006, McNew et al. 2012). Information on juvenile survival rates specifically for STGR is lacking. Therefore, we used a mean value of 0.40 for survival of juvenile birds from independence at 35 days of age to recruitment the following Spring (March 1). We also used an informative prior for first nest propensity for each stage class, using more conservative values than rates reported in the literature (beta(97, 5) for adults and beta(90,12) for yearlings) due to concerns about the potential for missing first nests that failed early during the laying period (Taylor et al. 2012, Coates et al. 2014). We assumed nest propensity was constant among years. Thus, fecundity was estimated as:

$$F_{ja} = ((np1_a * cl1_{ja} * ns1_a * h_a * cs_{ja} * js_a) + ((1-ns1_{ja}) * np2_{ja} * cl2_{ja} * ns2_{ja} * h_a * cs_{ja} * js_a))/2.$$

Subscripts reference year (j) and stage class (a). We divided the value of F by two because our model is female-based and we assumed an equal sex ratio, an assumption supported by the sample of captured adult birds (211 females and 220 males). We used an additive random effect structure to account for nesting female stage class and year.

Second nest propensity (np) was modeled as:

$$y_{np2,j} \sim \text{Binomial}(p_{np2,j}, n_{np2,j})$$

$$\text{logit}(p_{np2,j}) = \beta_{age,j} * x_{age,j} + \gamma_j$$

$$\gamma_j \sim \text{Normal}(0, \sigma_\gamma^2)$$

where $y_{np2,j}$ represents the number of renests, $n_{np2,j}$ is the number of unsuccessful first nests in each year (j) and $\text{logit}(p_{np2,j})$ is a function of female stage class ($\beta_{age,j}$) and random year effects (γ_j) drawn from a normal distribution with a mean of zero and a variance of σ_γ^2 .

The expected mean clutch size (μ_{cl}) at clutch c in year j is a linear function of random year effects (γ_j) and the change in the expected count of magnitude β_{age} , nesting female stage class. Clutch sizes of firsts nests and second nests were modeled as being drawn from a Poisson distribution and estimated as:

$$y_{cl,cj} \sim \text{Poisson}(\mu_{cl,cj})$$

$$\text{Log}(\mu_{cl,cj}) = \beta_{age} * x_{age,cj} + \gamma_j$$

$$\gamma_j \sim \text{Normal}(0, \sigma_\gamma^2)$$

Egg hatchability (h) was compiled from nests that were successful (one or more eggs hatched) and estimated as arising from a binomial distribution following the same equation for second nest propensity, where the initial clutch size represented the number of trials with a binary

outcome (hatch or not hatch) and the number of hatched eggs represented the number of successes. We included the same random effects for year and female stage class.

Chick survival (cs) was modeled based on flush counts of chicks at approximately 35 days post-hatch arising from a binomial distribution (logit-link function). The initial brood size represented the number of trials and chicks that survived to day 35 were the successes. The estimated model included random effects for year (γ_j) and female stage class (β_{age}) as well as parameters with indicators for grazing system (as described above; β_{grz1} and β_{grz2}). We assumed a constant hazard function and the model followed the form used for adult and nest survival and was estimated as:

$$y_{cs,j} \sim \text{Binomial}(p_{cs,j}, n_{cs,j})$$

$$\text{logit}(p_{cs,j,35}) = \beta_{age,j} * x_{age,j} + \beta_{grz1} * x_{grz1} + \beta_{grz2} * x_{grz2} + \gamma_j$$

$$\gamma_j \sim \text{Normal}(0, \sigma_\gamma^2)$$

Joint Likelihood—After defining the sub-models, we specified the joint likelihood which is the product of the component likelihoods of the population count data (from the N -mixture model), stage class survival data, and fecundity data. In concert, the subcomponents of the IPM were used to derive posterior distributions for STGR vital rates, and enabled us to estimate the total female population across the study area in each year. The mean expected number of recruits into the yearling stage class (μ_{1yi}) was estimated as:

$$\mu_{1yi} = N_{s(1,y-1,i)} * R_{(1,y-1)} * S_{8(1,y-1)} +$$

$$N_{s(2,y-1,i)} * R_{(2,y-1)} * S_{8(2,y-1)},$$

where subscripts a , y , and i correspond to stage class ($a = 1$ for yearlings and 2 for adults), year, and lek site respectively. N_s represents the initial number of each age class in each year at each lek site i . Symbols R and S_8 represent recruitment and eight-month survival. The number of yearling recruits (N_{1yi}) is:

$$N_{1yi} \sim \text{Poisson}(\mu_{1yi})$$

We represent the number of yearlings surviving into adulthood ($N_{\text{new}(2yi)}$) as being drawn from a Binomial distribution given the annual survival of yearlings from the previous year and the number yearlings from that lek the year before.

$$N_{\text{new}(2yi)} \sim \text{Binomial}(S_{12(1,y-1)}, N_{(1,y-1,i)})$$

Similarly, the number of surviving adults from the prior year ($N_{\text{old}(2yi)}$) is estimated as being drawn from a Binomial distribution with a mean of the annual adult survival from the year before and the number of adults from the lek the prior year, represented as:

$$N_{\text{old}(2yi)} \sim \text{Binomial}(S_{12(2,y-1)}, N_{(2,y-1,i)})$$

Given the information in the constructed Lefkovich matrix and abundance estimates for both stage classes, we estimated abundance at each lek in each year, where total adults (N_{2yi}) is the sum of new adults ($N_{\text{new}(2yi)}$) and returning adults ($N_{\text{old}(2yi)}$) and total abundance (N_{tot}) is the sum of total adults (N_{2yi}) and yearlings (N_{1yi}):

$$N_{(2yi)} = N_{\text{new}(2yi)} + N_{\text{old}(2yi)}$$

$$N_{\text{tot}} = N_{2yi} + N_{1yi}$$

Population totals across the study area are estimated by summing lek site totals for all leks in each year. From the derived abundance estimates, we calculated the finite rate of population change (λ ; Caswell 200, Gotelli and Ellison 2004) by dividing total abundance in year $j+1$ by the total abundance in the previous year j . Thus,

$$\lambda_j = \frac{N_{j+1}}{N_j}$$

where subscript j represents year. Posterior distributions of estimated parameters were summarized by mean and 95% credible intervals (CrI).

We used the packages *rjags* (Plummer 2019) in Program R (version 3.6.2; R Core Team 2019) with Markov chain Monte Carlo methods to obtain posterior samples of the parameters of interest, running three independent chains of 110,000 iterations, thinned by a factor of 5, after a burn-in of 10,000. Mixing was sufficient and convergence was achieved as confirmed by examining trace plots and R-hat values (all less than 1.01; Gelman et al. 2013) after estimation.

Results:

Estimated vital rates (Tables 13-15) from the IPM generally agree with those estimated from our previous independent analyses (Tables 1-5; Milligan 2019, Milligan et al. 2020a-c). For example, Milligan et al. (2020b) reported that the five-month breeding season survival across all years and grazing systems was 0.65 (SE = 0.04). Our five-month breeding season estimate for each year and stage class from the IPM ranged from 0.67 to 0.83. Annual survival rates for STGR in the literature range from 0.17 to 0.43 but have been reported as high as 0.71 (Robel et al. 1972, Connelly et al. 1998). Our annual survival estimates fall within this range, averaging 0.52 across stage classes and years, with the lowest estimated value being 0.38 (95% CrI: 0.23-0.54) for yearlings in 2017. Milligan et al. (2020b) reported annual survival rates and standard errors of 0.50 ± 0.05 in 2016, 0.28 ± 0.04 in 2017, and 0.46 ± 0.05 in 2018.

Consistent with our previous independent evaluations (Milligan et al. 2020a-c), estimates and credible intervals for the hazard ratios for the effect of the three grazing systems (summer rotation, rest-rotation, and season-long) indicate that grazing system did not impact key vital rates of our STGR population (Table 16). However, we are currently evaluating whether more explicitly linking the grazing system with discrete observations over time rather than as a majority classification, examining impacts on more fecundity parameters, and evaluating whether grazing system differentially affected the two stage classes of females. Inclusion of the effect of grazing system on more parameters and the temporal variation in use may allow us to detect a subtle but chronic impact of grazing system on vital rates and therefore, population dynamics.

Collectively, estimated rates of finite population change indicated a declining population between 2016–2018, with the largest decrease between 2017 and 2018 ($\lambda = 0.69$, 95% CrI: 0.54–0.84; Table 16); the last two years of the study corresponding to significant drought. Our desire is to estimate cumulative effects of grazing system on λ . However, STGR were not restricted to a single grazing system during an annual cycle (i.e., most radio-marked females were located in multiple grazing systems throughout the year), making assignments of a complete suite of vital rates, particularly annual survival, from a single female to a particular grazing system impossible.

Goals for next quarter:

During the first quarter of 2021, we will complete the IPM analysis and draft a manuscript for publication. Construction of the IPM required us to make certain assumptions about the population, such as an equal sex ratio. In the future, a sensitivity analysis would prove useful in illuminating whether violation of these assumptions translates to significant changes in estimated parameters, as well as informing us about the most critical vital rates in this population of STGR. This information would be valuable in assisting biologists and managers in making informed decisions prior to management actions and predicting the outcome in terms of changes in STGR populations.

Objective 2: Investigate impacts of rest-rotation grazing on sharp-tailed grouse home ranges, movements and habitat selection.

Accomplishments

All field work related to Objective 2 were completed during 2016–2018. Efforts in 2020 focused on analyzing data and writing publications of our work. Below we summarize effort and results for the entire 4-year study. Comprehensive results are also reported in:

Milligan, M.C. 2019. Effects of grazing management on sharp-tailed grouse ecology in mixed-grass prairies. Dissertation, Montana State University, Bozeman, Montana, USA.

Milligan, M.C. †, L.I. Berkeley, and L.B. McNew. 2020. Habitat use of sharp-tailed grouse in rangelands managed for livestock. *PloSOne* 15(6): e0233756.

Milligan, M.C. †, L.I. Berkeley, and L.B. McNew*. 2020. Effects of rangeland management on the nesting ecology of sharp-tailed grouse. *Rangeland Ecology and Management* 73:128–137.

Methods

Radio-marked females were located by triangulation or homing ≥ 3 times/week during the breeding season (15 March – 15 August). Coordinates for triangulated locations were calculated using Location of a Signal software (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary) and examined for spatial error. All locations with low estimation precision (> 200 m error ellipse) were discarded.

We analyzed location data for the breeding season (15 March – 15 August) and defined a home range as the space an individual needed to forage, reproduce, and survive. Previous studies have found that small sample sizes can bias home range estimates (Seaman et al. 1999), so analyses were restricted to birds with ≥ 30 locations and ≥ 20 locations not associated with a nest site. We used the fixed kernel method [56] with the default smoothing parameter to calculate home ranges as the 95% utilization distribution for the breeding season (April – August) using the *adehabitatHR* package in Program R. We also calculated centroids for each home range by estimating the 1% volume contour of each home range and using the geographic center of that contour as the centroid.

We used linear models to evaluate the relationship between home range size and the effects of year; nest outcome; density of edge habitat within the home range; proportion grassland within the home range; proportion of each grazing system contained within the home range; mean stocking rate within the home range; and distance to nearest lek, grassland patch edge, road, and

oil pad at the home range centroid. We calculated the proportion of grassland and edge density within each home range in ArcGIS and measured the distance from each centroid to the nearest lek, grassland patch edge, road and oil pad in Program R 3.5.1. Habitat classifications utilized the 30-m resolution LANDFIRE data depicting landcover type (LANDFIRE 2013). A habitat patch edge was defined as an abrupt change between any of the three main landcover types (grassland, wooded draws, and cropland) and edge density was defined as the amount of patch edge relative to the home range size. We digitized the location of oil pads and roads in the study area and roads were defined as paved and dirt state and county roads and did not include ranch two-tracks. We collected information on grazing management for every pasture in the study area by interviewing landowners to determine the number and class of animals stocked and the timing of stocking to determine the grazing system (rest-rotation, summer rotation, season-long) and stocking rate (AUM ha⁻¹) during the current and previous year. Stocking rate is a measure of the number of animals in a pasture during the entire grazing season. As most females used more than one grazing system, we calculated the proportion of each individual home range containing the three different grazing systems and assigned a female to the grazing system containing $\geq 60\%$ of the home range. Females were considered to use multiple systems if no one system accounted for $\geq 60\%$ of their home range and were not included in analyses evaluating the effect of grazing system.

We examined second-order habitat selection, or the selection of habitat for an individual's home range within the larger study area, using the adehabitat package in Program R 3.5.1 to conduct compositional analysis of used versus available habitat (Johnson 1980, Aebischer et al. 1993). Available habitat was defined as the home range calculated for locations of all radio-marked females in a given year, whereas used habitat was measured within each individual home range. We used compositional analysis to compare used versus available landcover types and grazing systems separately. Landcover classifications were based on LANDFIRE data and were grouped into grassland, wooded draws, cropland, and other, which was composed primarily of ruderal grasslands (LANDFIRE 2013).

To evaluate third-order habitat selection, or the selection of habitat within individual home ranges, we used resource selection functions to compare used and available points following Design 3 of Manly et al. (2002). We identified nine landscape metrics *a priori* that could influence sharp-tailed grouse space use. Three of those metrics were related to rangeland management: grazing system and stocking rate (AUM ha⁻¹) during either the current or previous year. Two landscape metrics represented anthropogenic disturbance, including both oil pads and roads, and we calculated the distance to each from both used and available points. Four additional landscape variables were related to landcover: % grassland, % wooded draws, % cropland, and the density of edge habitat (total landcover edge length / polygon area), which were based on the 30-m resolution LANDFIRE data depicting landcover type (LANDFIRE 2013). We used FRAGSTATS 4.2 (McGarical et al. 2012) to conduct a moving window analysis to calculate the proportion of each landcover type and the density of edge habitat within 8 buffer distances (30, 75, 125, 200, 500, 750, 1000, 1300 m) to evaluate the spatial grain for each landcover type that best predicted grouse space use (Laforge et al. 2015). We chose grain sizes to reflect a continuum of scales, with 30 m representing the minimum size as imposed by our spatial data and 1,300 m approximating the average size of the breeding season home range of a female sharp-tailed grouse in our study area. A grain size of 200 m represents the average distance moved daily by female sharp-tailed grouse during the breeding season in our study. The

remaining grain sizes represent intermediate distances between the minimum imposed by our spatial data and a grain size representing the average size of a breeding season home range.

We conducted 1,000 simulations for each variable and each grain size of landcover variables to determine the number of available points required for coefficient estimates to converge (Northrup et al. 2013). Based on the simulations, available points were sampled at a 15:1 available:used ratio within each individual bird's home range to balance coefficient convergence and computational efficiency. For all models, we used generalized linear mixed models in a Bayesian framework with a logit-link and female ID as a random intercept to account for potential autocorrelation among sampling points (Gillies et al. 2006, Thomas et al. 2006). For the four landcover covariates, we first selected the grain size at which selection was the strongest for each, basing model selection comparing the 8 buffer distances on calculated leave-one-out information criterion (LOOIC) to identify a top model *sensu* Laforge et al. (2015). If error estimates overlapped for calculated LOOIC, we based model selection on calculated deviance information criteria (DIC) and considered > 5 DIC units to be a substantial difference in model fit (Thomas et al. 2006).

After assessing collinearity for each pair of explanatory variables ($r \geq 0.6$) and selecting the variable with the most support based on calculated LOOIC and DIC, we then evaluated support for all management and landscape variables in a full model using indicator variables. Regression coefficients for each variable were the product of binary indicator variables and both continuous and categorical covariates and we used the posterior distributions of the indicator variables to identify the variables with high inclusion probability that were the most important predictors of habitat selection [64-66]. We assumed that all variables with high inclusion probability based on the posterior distributions of their indicator variables influenced habitat selection and variables with inclusion probabilities ≤ 0.25 were unimportant (Mutshinda et al. 2013). The posterior distributions of coefficients represented the relationship between habitat variables and the relative probability of selection within the defined home range. We calculated standardized coefficients of fixed effects to make population-level inferences about each habitat variable and improve model convergence. Coefficients with 95% credible intervals that did not overlap zero were considered important. We examined estimates of variability (σ^2) for each predictor variable to determine the degree of variation in selection among individuals for specific habitat features (Indermaur et al. 2009).

We fit models using Markov Chain Monte Carlo (MCMC) simulations with JAGS (version 4.2.0, mcmc-jags.sourceforge.net, accessed Dec 2018) implemented via the 'runjags' package (Denwood 2006) in Program R 3.5.1 to approximate the posterior probability distribution of model parameters. Vague uniform or normal priors were used for all model parameters related to covariates and their measures of error (Kery 2010). Indicator variables were Bernoulli random variables and we placed a Beta(2,2) prior distribution on the inclusion probability of each indicator variable to represent no prior information about the importance of individual variables. We first identified the top spatial grain model for each landcover variable from 20,000 samples, thinned by a factor of 5, from 3 independent MCMC chains, after discarding 10,000 burn-in samples. Inference from the full model was based on a total of 50,000 samples, thinned by a factor of 5, from 3 independent MCMC chains, after discarding the first 100,000 burn-in samples. We assessed convergence and MCMC chain mixing visually and based on Gelman-Rubin convergence statistics and considered sets of chains with no trends across trace plots and values < 1.1 converged (Gelman 2006). To perform posterior predictive checks, we calculated a

Bayesian p -value as a goodness-of-fit measure that compares attributes of the observed data to that of data generated by the model (Gelman et al. 1996).

Nest site selection.— We examined habitat and management variables influencing nest site selection in separate analyses using resource selection functions. Habitat variables were considered for their direct effect on nest site selection, while management variables were considered for potential indirect effects on vegetation structure as mediated through livestock grazing practices. Nests were considered used sites and, as we did not conduct searches for nests of unmarked grouse, random points were considered available following Design 2 of Manly et al. (2002), where availability is defined at the population level. For each analysis, we used generalized linear mixed models with the logistic link function, a binomial error structure, and female ID as a random effect to account for potential autocorrelation. Before fitting models, we examined correlations for each pair of explanatory variables ($r \geq 0.6$) and if two variables were highly collinear, we used single factor logistic regression to determine which variable accounted for more of the variation in the data. All preliminary analyses are reported in the appendices. Models were compared using AICc and model selection was based on both minimization of AICc and AICc weights (w_i). For the habitat-level analysis, we first evaluated underlying variables, variables at the nest-site scale, and variables at the home-range scale independently and built a final candidate model set that included variables supported at each scale. Underlying variables included year, hen age, and nest attempt. Variables at the nest-site scale included VOR at the nest bowl and averaged within the 6 m radius plot, distance to grassland edge, and the percentage of shrubs, new grass, residual grass, forbs, and bare ground. Different functional relationships with VOR were examined, including linear, quadratic and natural log models (i.e., pseudo-threshold effects; Dugger et al. 2005; McNew et al. 2014). Variables considered at the home-range scale included the proportion of grassland habitat, density of edge habitat, grassland shape complexity (MSI), and distance to oil pad, road, or lek. We then selected the most parsimonious models at each of the different spatial scales (nest-site and home range level) and assessed them in the final candidate model set. In the management-level analysis, we evaluated all combinations of the effects of grazing system and stocking rate. We also evaluated additive and interaction models with year and either grazing system or stocking rate to assess whether a system-level effect was only apparent under certain annual conditions. Variables were considered significant if 85% confidence intervals did not overlap zero (Arnold 2010). Finally, we evaluated combinations of important variables from both the habitat- and management-level analyses into a final candidate model set to assess the relative importance of habitat and management variables.

For the top RSF, we calculated the marginal and conditional R^2 to evaluate the total variance explained by the model (Nakagawa and Schielzeth 2013). We validated the top RSF with a reserved data set of 39 randomly selected nests sites and 39 random points (20% of data; Boyce et al. 2002). The top model was used to calculate predicted RSF values for each nest in both the training and the test data sets. Raw RSF values were placed in 5 quantile bins representing an increasing likelihood of a point being classified as a nest site. We regressed the proportion of nests from the test data set in each bin against the proportion of nests from the training data set in each bin and evaluated good model fit based on Johnson et al. (2006).

Results

During the 2016–2018 breeding seasons, we collected a total of 7,178 locations and calculated 142 home ranges for 118 individual females (40 in 2016, 53 in 2017, 49 in 2018). Home range

size was estimated without bias relative to sampling effort (Milligan 2019). Mean breeding season home range size for all females was 489 ± 41 ha but varied from 58–3,717 ha (Table 9). Home range sizes were less variable within pastures managed with summer rotation grazing compared to those in other systems (Fig 8), but grazing system did not have a significant effect on average size of home ranges (Table 10). Density of edge habitat within the home range was the best predictor of home range size (Table 10) and was negatively related to the size of breeding season home ranges ($\beta = -5.26 \pm 1.48$; Fig 9).

At the second order, breeding season habitat use was ranked as follows: grassland = wooded draws >> other (primarily ruderal grasslands) >> cropland (Table 11), suggesting that females did not differentiate between grasslands and wooded draws with regards to preference but selected both habitat types over other habitats, including cropland. Females strongly selected for mixed grass prairie habitats, even though roughly 83% of the entire study area was composed of mixed grass prairie. Females strongly selected against cropland during the breeding season, even though only 4% of the study area was cropland. There was no evidence that selection of home ranges in relation to grazing system was different from random ($p = 0.20$), suggesting that females were not differentiating between pastures in the different grazing systems.

Within home ranges, preliminary analyses suggested that a grain size of 1,300 m for grassland, 1,300 m for wooded draws, 500 m for cropland, and 1,000 m for edge density represented the scale of strongest female habitat selection (Milligan 2019). However, the proportion of grassland was correlated with both the proportion of cropland and the density of edge habitat (see Supporting Information), so only the variable of proportion grassland was used in the full model. In the full analysis, distance to road and the proportion of wooded draws within 1,300 m were the only supported covariates, with indicator values > 0.25 (Fig 10). Only distance to road had a 95% credible interval that did not overlap zero ($\beta = -0.047 \pm 0.001$), although differences in selection across the range of distances were small (Fig. 11). Furthermore, variability in selection as measured by σ^2 for each predictor variable was high, indicating large differences in individual habitat selection (Fig. 12). A posterior predictive check suggested that the full model fit the data well, based on an estimated Bayesian p-value of 0.503.

Nest site selection.— We located 188 grouse nests (147 first nests, 41 renesting attempts) laid by 128 individual females during 2016–2018. None of the underlying variables, including year, female age and nest attempt, improved model fit over the null model. Preliminary analyses suggested that visual obstruction at the nest bowl best predicted nest site selection and that a pseudo-threshold model best represented the relationship between visual obstruction and nest site selection, so only models with the natural log transformation of nest VOR were included in analyses (Milligan 2019). At the nest-level, nest site selection was best predicted by VOR at the nest bowl and the percentage of new grass, residual grass, and shrubs ($\Delta AICc = 0$, $w_i = 0.61$). At the home-range level, the model containing a measure of fragmentation (mean shape complexity or MSI) received the most support ($\Delta AICc = 0$, $w_i = 0.56$). In the final candidate model set, the model that included VOR at the nest bowl, the percentage residual grass, and MSI received the most support ($\Delta AICc = 0$, $w_i = 0.61$, Table 12). Confidence intervals for VOR, MSI, and proportion residual grass and shrubs did not overlap zero, suggesting significant effects (Fig. 13). Percent cover of both residual grass ($\beta = 0.48 \pm 0.17$) and shrubs ($\beta = 0.33 \pm 0.20$) had small but positive effects on the relative probability of selection, while selection decreased with increasing fragmentation or MSI ($\beta = -0.50 \pm 0.16$). Visual obstruction at the nest bowl had the largest

effect on the relative probability of selection ($\beta = 11.45 \pm 1.31$), with selection increasing up to a threshold of 20–30 cm (Fig. 13).

In the management-level analysis, models containing the linear effect of stocking rate from the previous year received the most support ($w_i = 0.51$, Table 12), with 85% confidence intervals that did not overlap zero. The relative probability of selection declined with increasing stocking rates ($\beta = -0.17 \pm 0.10$). However, in the full analysis, the model containing habitat variables ($\Delta AICc = 0$, $w_i = 0.58$) outperformed models with management-level variables (Table 12), with an evidence ratio for the model containing only habitat variables compared to the combined habitat and management model of 1.38. This suggests that grazing management was not an important predictor of nest site selection after controlling for other factors.

The marginal and conditional R^2 for the top model were both 0.97. Model validation based on linear regression suggested high predictive accuracy, with an intercept of 0 (95% CI: -0.02–0.06), slope of 0.91 (95% CI: 0.76–1.06), and a high coefficient of determination ($R^2 = 0.87$).

Objective 2a: Evaluate habitat selection by sharp-tailed grouse broods in relation to ecological site condition

Two common limitations of rangeland wildlife habitat research to date are that 1) the scale of habitat variables assessed rarely matches the scale of population response to land management actions and 2) wildlife researchers often do not directly evaluate the ecological indicators on which rangeland managers make decisions. For example, previous assessments of habitat preferences of prairie-grouse typically focus on individual responses to local scale habitat conditions (e.g., grass height at nest sites; McNew et al. 2013), but rangeland management decisions are based on a different set of ecological or habitat indicators (e.g., ecological site type and condition) and management actions occur at the scale of a pasture or ranch, not a nest site.

To address these disconnects and provide relevant habitat management recommendations for rangeland managers, we evaluated the habitat selection patterns of sharp-tailed grouse broods at multiple orders of selection in relation to ecological site types and their relative condition. An ecological site has specific characteristics that differ from other types of land in its ability to support a distinct kind and amount of vegetation (United States Department of Agriculture, 2006). Ecological sites also vary in their ability to respond to natural disturbances and management practices because they integrate information about landscapes using both geophysical and biotic components including soil, climate, hydrology, landscape position, plant species occurrence, and plant community composition. Ecological site descriptions (ESDs) are developed by the US Department of Agriculture Natural Resource Conservation Service (NRCS) at the state level and serve as a framework for making informed site-specific land management decisions (Herrick et al., 2006). Although ESDs do not reflect recent plant community changes caused by management and disturbances, they represent historic climax plant communities believed to dominate the site before Euro-American settlement. The potential productivity and composition of a site can be estimated by comparing the current plant community to the historic plant community using a similarity index, which can describe the extent of change on a site from its original condition. The similarity index, or “relative condition” can be measured over time to evaluate the effects of management activities (United States Department of Agriculture, 2006).

Though widespread in rangeland ecology and management, the use of ESDs to assess habitat suitability or predict habitat selection in wildlife is uncommon (Anderson et al. 2015; Braunisch and Suchant 2008, Hibbs 2011, Kraft 2012). Because ESDs encompass structural site

characteristics, they have proved useful in evaluating songbird density and diversity in the sagebrush steppe (Williams et al. 2011) and to predict winter habitat use by greater sage-grouse (*Centrocercus urophasianus*); though they were not useful metrics to predict nest site occurrence and nest survival (Doherty et al. 2011, Woodward 2006). Collectively, these findings suggest potential but species- and scale-dependent associations between wildlife populations and ESDs. A limitation of work to date is that the relative condition of ESDs has not been considered when evaluating wildlife-ESD associations and may explain some potential inconsistencies.

We studied hierarchical habitat selection of radio-marked sharp-tailed grouse in the northern mixed-grass prairie of eastern Montana during 2016–2018 to evaluate associations with common rangeland indicators: ESDs and their relative condition (i.e., similarity index). Female prairie-grouse have previously been found to select heterogeneous habitats during the breeding season characterized by variation in biotic and abiotic characteristics (McNew et al. 2014, Milligan et al. 2020) and previous work has found strong associations between habitat use and vegetation conditions at multiple spatial scales (McNew et al. 2013). If ESDs and their relative condition determine vegetation communities, we expected to find significant interactive effects of these habitat descriptors on brood habitat selection of both home ranges within the study area (second-order selection; Johnson, 1980) and fine-scale selection of use sites within home ranges (third-order selection). We hypothesized that ESDs selected by broods would be characterized by greater heterogeneity in vegetation conditions, especially the proportion of forbs and visual obstruction reading (VOR) which correspond to food resources and cover for prairie-grouse broods.

Methods

We monitored radio-marked female sharp-tailed grouse with broods as described above. We obtained a map of ecological sites and their accompanying ecological site descriptions (ESDs) from the USDA-NRCS office in Richland County, Montana. ESD information was collected by rangeland conservationists and soil scientists employed by the USDA-NRCS. Detailed methodology for delineating and classifying ecological sites can be found in Chapter 4 of the National Range and Pasture Handbook (United States Department of Agriculture, 2006). Doherty et al. (2011) provides a more in-depth explanation of the protocols and procedures used by USDA-NRCS rangeland conservationists for determining ecological site classifications and descriptions.

We measured the condition within each different ecological site by using a similarity index to compare the current plant community to the historic plant community. Quantitative descriptions of historic plant communities were obtained from the ESDs. Similarity index for each ecological site was assessed between June 18th, 2018 and July 4th, 2018. At ten random locations in the study area, vegetation in a 1 m by 1m plot was clipped and divided into two bags. One bag contained only decreaser grass species while the other contained all other vegetation (increaser grasses, forbs, shrubs, etc.). Before weighing the bags, we visually estimated the percent decreaser grass species contained in the plot. Both bags were weighed and normalized to estimate percentage dry weight of plant material at the current growth stage. The similarity index was then calculated by comparing the weight to the decreaser graminoids to all other clipped vegetation. The purpose of this exercise was to calibrate our observations in order to measure percent decreaser graminoid visually. We conducted pasture-level surveys by walking pastures and estimating similarity index for each ESD polygon at a scale of 1 ha or greater

(Source). The similarity index was divided into 5 classes: very low, low, moderate, high, and very high. We then digitized maps of similarity index using ArcMap 10.6.1.

We evaluated local habitat conditions at a subset of brood locations as well as at paired random locations. At these sites, we record visual obstruction readings (VOR) at the center of the brood location and at four points 6 m from the center in each cardinal directions. VOR was measured at each point in all four cardinal directions from a distance of 2 m and a height of 0.5 m using a Robel pole (Milligan et al., 2020; Robel et al., 1970). We also estimated non-overlapping vegetation cover classes (percent new grass, residual grass, forbs, shrubs, bare ground, and litter) at 12 subsampling points within 6 m of the brood site using Daubenmire methods (Daubenmire, 1959).

Statistical Analyses

2nd Order Selection. – We examined second order selection, or selection of habitat for an individual's home range within the study area, using resource selection functions. Available habitat was defined as the 95% home range calculated for all locations across all three years within the study area using the adehabitat package in Program R (Aebischer et al. 1993). Random points were plotted inside this study area home range at a 1:40 ratio of used:available points. We transformed similarity index from a discrete variable with 5 classes to a continuous variable by using the midpoint value for each class. For each analysis, we used generalized linear models with a logit link function. We evaluated the effects of ecological site type, similarity index, as well as the additive and interaction effects of the two. Models were then compared using Akaike's Information Criterion (AIC_c) and the most parsimonious model was selected as our top model.

In addition to using resource selection functions and model selection, we also used the rank analysis procedure outlined by Johnson et al. (1980) to determine if ecological site type played a role in second order habitat selection. We subset our data to include broods which had 12 or more used locations to match the number of ecological site classes found in the study area. Preference was determined by the difference between the rank of used locations and the rank of available locations. We used a Kruskal-Wallis test to determine if the ranks were significantly different from each other and a pairwise Wilcoxon rank sum test to analyze difference among ecological site classes.

3rd Order Selection. – We examined the effect of ecological site type and similarity index of ecological sites on brood site selection using resource selection functions. Because we did not conduct searches for unmarked grouse broods, brood sites of marked birds were considered used and random points were considered available following Design 3 of Manly et al. (2002), where a home range is defined for each individual and available points are sampled within the home range. Home ranges were calculated using the adehabitat package in Program R for broods with greater than 4 locations. Broods that had less than 5 locations were buffered by 200 m, which was the average distance moved by female grouse during the breeding season in our study. Random points were plotted inside each brood's home range at a 1:40 ratio of used:available points. Ecological site type and similarity index class were extracted to each used and available point in ArcMap 10.6.1. We transformed similarity index from a discrete variable with 5 classes to a continuous variable by using the midpoint value for each class. To determine if we should include brood ID as a random effect to account for autocorrelation, we compared conditional and marginal R² values for generalized linear models with and without the random effect and found

no difference, which led us to drop the random effect. We examined different functional relationships with similarity index including linear, quadratic, and logarithmic models and compared them using AIC_c . The linear model was the top model, so we only included this relationship in our candidate model set. The effects of ecological site class, similarity index class, and their additive and interaction effects were assessed, and AIC_c was used to select our top model.

Results

We collected 845 brood locations from 97 individual broods during 2016–2018. There were 12 different ecological sites found in our study area, but only 10 had brood locations. Three ecological sites comprised 88% of the study area and 98% of the study area had a similarity index of less than 60%.

Second Order Selection

For selection of a home range, habitat selection was best predicted by the interaction between ecological site type and similarity index ($\Delta AIC_c = 0$, $w_i > 0.99$), suggesting that the effects of ecological site were mediated by the relative condition of the site. Due to singularities, the interaction model could only be fit for 6 out of the 10 ecological sites in the study area that contained brood locations.

For the gravelly ($\beta = 0.0057 \pm 0.9947$), shallow-loamy ($\beta = 0.0681 \pm 0.6743$), loamy-rolling soft shale ($\beta = 0.1977 \pm 0.7923$), and silty sedimentary sites ($\beta = 0.2795 \pm 0.6385$), relative probability of selection decreased as similarity index increased. However, for the limy residual ($\beta = 0.9453 \pm 0.8005$) and saline lowland sites ($\beta = 0.9986 \pm 0.9629$), relative probability of selection increased as similarity index increased.

Third Order Selection

For selection within a home range, habitat selection was best predicted by similarity index ($\Delta AIC_c = 0$, $w_i = 0.81$). In fact, the top three models all contained similarity index, either independently as with the top model, or in the interaction and additive models. Relative probability of selection decreased as similarity index increased ($\beta = 0.3140 \pm 0.5554$).

We found little evidence that ecological site type had any effect on brood habitat selection within a home range ($\Delta AIC_c = 10.5$, $w_i = 0.00$). Relative probability of selection did not significantly differ between ecological sites.

Goals for next quarter

We will finalize our brood habitat use analysis and draft a manuscript for publication in the journal *Rangeland Ecology and Management*.

Objective 3: Develop a mechanistic understanding of the ecological effects of various grazing treatments with a focus on rest rotation grazing by examining abundance and space use of the grassland bird and mesopredator communities

Project completed. Complete results are presented in previous Annual Progress Reports and the following publications:

- Vold, S. T. 2018. Effects of livestock grazing management on the ecology of grassland birds and their predators in a northern mixed-grass prairie ecosystem. Thesis, Montana State University, Bozeman, Montana, USA.
- Vold, S.K., L.I. Berkeley, and L.B. McNew. 2019. Effects of livestock grazing management on grassland birds in a northern mixed-grass prairie ecosystem. *Rangeland Ecology and Management* 72:933–945.

Literature Cited

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.
- Andersen, P. K., and R. D. Gill. 1982. Cox's regression model for counting processes: a large sample study. *Annals of Statistics* 10:1100-1120.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175-1178.
- Burnham, K. P., and D. R. Anderson. 2002. A practical information-theoretic approach. Springer, New York, NY, USA.
- Caswell, H. 2001. Matrix population models. Sinauer Associates, Inc. Sunderland, MA, USA.
- Coates, P.S., B. J. Halstead, E. J. Blomberg, B. Brussee, K. B. Howe, L. Wiechman, J. Tebbenkamp, K. P. Reese, S. C. Gardner, and M. L. Casazza. 2014. A Hierarchical Integrated Population Model for Greater Sage-Grouse in the Bi-State Distinct Population Segment, California and Nevada. USGS Open-File Report 2014-1165.
- Connelly, J. W., M. W. Gratson, and K. P. Reese. 1998. Sharp-tailed Grouse (*Tympanuchus phasianellus*). *The birds of North America*:20.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43-64.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476-3488.
- DelGiudice, G. D., J. Fieberg, M. R. Riggs, M. C. Powell, and W. Pan. 2006. A long-term age-specific survival analysis of female white-tailed deer. *Journal of Wildlife Management* 70:1556-1568.
- Denwood M.J. 2016. runjags: An R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. *Journal of Statistical Software* 71:1-25.
- Dugger, K. M., F. Wagner, R. G. Anthony, and G. S. Olson. 2005. The relationship between habitat characteristics and demographic performance of northern spotted owls in southern Oregon. *The Condor* 107:863-878.
- Fox, J. 2002. An R and S-PLUS companion to applied regression. SAGE Publications, Los Angeles, CA, USA.
- Gelman A, and J. Hill. 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK.
- Gelman A, X.L., and H. Stern. 1996. Posterior predictive assessment of model fitness via realized discrepancies. *Statistica sinica* 6:733-60.
- Gillies, C.S., M. Hebblewhite, S.E. Nielsen, M.A. Krawchuk, C.L. Aldridge, and J.L. Frair. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75(4):887-98.

- Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2013. Bayesian data analysis. CRC Press, Boca Raton, FL, USA.
- Goddard, A. D., and R. D. Dawson. 2009. Seasonal changes in habitat features influencing nest survival of sharp-tailed grouse in northeastern British Columbia, Canada. *Ecoscience* 16:476-482.
- Gotelli, N. J. and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer Associates, Inc., Sunderland, MA, USA.
- Goddard, A. D., R. D. Dawson, and M. P. Gillingham. 2009. Habitat selection by nesting and brood-rearing sharp-tailed grouse. *Canadian Journal of Zoology* 87:326-336.
- Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* 82:1473-1483.
- Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2006. Radiotelemetry survival estimates of lesser prairie-chickens in Kansas: Are there transmitter biases? *Wildlife Society Bulletin* 34:1064-1069.
- Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2009. Spatial variation in lesser prairie-chicken demography: a sensitivity analysis of population dynamics and management alternatives. *The Journal of Wildlife Management* 73: 1325-1332.
- Halstead, B. J., G. D. Wylie, P. S. Coates, P. Valcarcel, and M. L. Casazza. 2012. Bayesian shared frailty models for regional inference about wildlife survival. *Animal Conservation* 15: 117-124.
- Hooten, M. B., E. M. Hanks, D. S. Johnson, and M. W. Alldredge. 2013. Reconciling resource utilization and resource selection functions. *Journal of Animal Ecology* 82:1146-1154.
- Indermaur, L., T. Winzeler, B.R. Schmidt, K. Tockner, M. Schaub. 2009. Differential resource selection within shared habitat types across spatial scales in sympatric toads. *Ecology* 90:3430-44.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Johnson, C. J., M. S. Boyce, C. C. Schwartz, and M. A. Haroldson. 2004. Modeling survival: application of the Andersen–Gill model to Yellowstone grizzly bears. *Journal of Wildlife Management* 68:966-978.
- Kéry, M. 2010. Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press; Cambridge, MA, USA.
- Kéry, M. and M. Schaub. 2011. Bayesian population analysis using WinBUGS; a hierarchical perspective. Academic Press; Cambridge, MA, USA.
- Laforge, M.P., W.E. Vander, R.K. Brook, E.M. Bayne, P.D. McLoughlin. 2015. Process-focused, multi-grain resource selection functions. *Ecological Modeling* 305:10-21.
- LANDFIRE. 2013. LANDFIRE Existing Vegetation Type layer. U. S. Department of Interior, Geological Survey. Available: <http://www.landfire.gov/index.php> [2016, November 18].

- Manly, B., L. McDonald, D. Thomas, T. McDonald, and W. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. Nordrecht, The Netherlands: Kluwer.
- Marzluff, J. M., J. J. Millsbaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. *Ecology* 85:1411-1427.
- McGarigal, K., S.A. Cushman, E. Ene. 2012. FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst, USA; <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2012. Demography of greater prairie-chickens: Regional variation in vital rates, sensitivity values, and population dynamics. *Journal of Wildlife Management* 76:987-1000.
- McNew, L. B., L. M. Hunt, A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2014. Effects of wind energy development on nesting ecology of greater prairie-chickens in fragmented grasslands. *Conservation biology* 28:1089-1099.
- Milligan, M.C. 2019. Effects of grazing management on sharp-tailed grouse ecology in mixed-grass prairies. Dissertation, Montana State University, Bozeman, Montana, USA.
- Mutshinda, C.M., Z.V. Finkel, and A.J. Irwin. 2013. Which environmental factors control phytoplankton populations? A Bayesian variable selection approach. *Ecological Modeling* 269:1-8.
- Northrup, J.M., M.B. Hooten, C.R. Anderson Jr., G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology* 94(7):1456-63.
- Pitman, J. C., C. A. Hagen, B. E. Jamison, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2006. Survival of juvenile lesser prairie-chickens in Kansas. *Wildlife Society Bulletin* 34:675-681.
- Plummer, M. 2019. rjags: Bayesian Graphical Models using MCMC. CRAN.R-project.org/package=rjags.
- Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *The Condor* 109:949-954.
- R Core Team. 2019. R: A Language and Environment for Statistical Computing. Vienna, Austria. R-project.org
- Robel, R., J. Briggs, A. Dayton, and L. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295-297.
- Robek, R. J., F. R. Henderson, and W. Jackson. 1972. Some sharp-tailed grouse population statistics from South Dakota. *The Journal of Wildlife Management*: 87-98.
- Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60: 108-115.

- Seaman, D. E., J. J. Millsbaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *The journal of wildlife management* 63:739-747.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*. Blackburn Press, Caldwell, NJ, USA.
- Schaub, M. and F. Abadi. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology* 152: 227-237.
- Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. *The Journal of Wildlife Management* 76: 336-347.
- Thomas, D.L., D. Johnson, and B. Griffith. 2006. A Bayesian random effects discrete-choice model for resource selection: Population-level selection inference. *Journal of Wildlife Management* 70:404-12.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird study* 46:S120-S139.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.
- Zipkin, E. F., and S. P. Saunders. 2018. Synthesizing multiple data types for biological conservation using integrated population models. *Biological Conservation* 217: 240-250.

Table 1. Demographic rates estimated for sharp-tailed grouse.

Demographic Rate	Description
Nesting rate (NEST)	The probability of a female initiating a nest.
Clutch size (CS)	The final clutch size per nest. Estimates generated for both first (CS ₁) and renesting (CS ₂) attempts.
Nest survival (NSURV)	The probability of a nest producing ≥ 1 chick.
Renesting rate (RENEST)	The probability of a female initiating a replacement nest after failure of the first attempt
Chicks per egg laid (CPE)	The proportion of eggs laid that produced chicks, or the viability of the eggs; calculated only for successful nests (≥ 1 egg hatched).
Brood survival (BSURV)	The probability that ≥ 1 chicks survived to fledging at 14-d post-hatch
Fledglings per chick hatched (FPC)	The proportion of hatched chicks that survived to fledging conditional upon brood survival

Table 2. Total number of sharp-tailed grouse captured and radio-marked during the study, 2016-2018. Easement refers to leks occurring in pastures managed with rest-rotation grazing.

	Males	Females	New Radio-marked Females
Easement	119	121	89
Reference	101	90	85
Total	220	211	174

Table 3. Support for models predicting sharp-tailed grouse nest survival in 2016-18 in the three analyses examining habitat-level variables, management-level analyses and the combined analysis. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and deviance are reported. VOR is visual obstruction averaged across the 6 m radius vegetation plot.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Deviance
<u>Habitat Analysis</u>					
ln(VOR) + %Forb + Prop. Grassland	4	747.5	0	0.43	739.49
ln(VOR) + Prop. Grassland	3	748.94	1.44	0.21	742.94
ln(VOR) + %Residual + Prop. Grassland	4	750.94	3.44	0.08	742.93
ln(VOR) + %New Grass + Prop. Grassland	4	750.94	3.44	0.08	742.93
ln(VOR) + %Forb + Dist. to Road	4	751.64	4.14	0.05	743.63
ln(VOR) + Dist. to Road	3	751.71	4.21	0.05	745.7
ln(VOR)	2	753.59	6.09	0.02	749.59
ln(VOR) + %New Grass + Dist. to Road	4	753.62	6.12	0.02	745.61
ln(VOR) + %Residual + Dist. to Road	4	753.69	6.19	0.02	745.68
ln(VOR) + %Forb	3	754.09	6.59	0.02	748.08
ln(VOR) + %Residual	3	755.41	7.91	0.01	749.41
ln(VOR) + %New Grass	3	755.42	7.92	0.01	749.42
Dist. to Road	2	757.17	9.68	0	753.17
Prop. Grassland	2	758.53	11.03	0	754.53
Null	1	758.94	11.44	0	756.94
<u>Management Analysis</u>					
Stocking Density	2	755.05	0	0.24	751.05
Stocking Rate (cur. yr.) + Year + Stocking Density	5	755.1	0.05	0.23	745.08
Stocking Rate (prv. yr.) + Year + Stocking Density	5	755.56	0.51	0.19	745.54
Grazing System + Year	5	757.17	2.12	0.08	747.15
Stocking Rate (cur. yr.) + Year	4	757.2	2.15	0.08	749.19
Stocking Rate (prv. yr.) + Year	4	757.3	2.25	0.08	749.29
Null	1	758.94	3.89	0.03	756.94
Grazing System	3	760.18	5.13	0.02	754.17
Stocking Rate (cur. yr.)	2	760.49	5.44	0.02	756.49
Stocking Rate (prv. yr.)	2	760.9	5.85	0.01	756.89
Stocking Rate (cur. yr.) + Grazing System	4	761.85	6.8	0.01	753.84

Stocking Rate (prv. yr.) + Grazing System	4	762.16	7.11	0.01	754.14
Grazing System * Year	9	763.24	8.19	0	745.19
Stocking Rate (cur. yr.) * Grazing System	6	765.83	10.78	0	753.81
Stocking Rate (prv. yr.) * Grazing System	6	765.84	10.79	0	753.82
Full Analysis					
ln(VOR) + Prop. Grassland + Stocking Density	4	743.56	0	0.9	735.55
ln(VOR) + Prop. Grassland	3	748.94	5.38	0.06	742.94
ln(VOR) + Prop. Grassland + Grazing System + Year	7	749.82	6.26	0.04	735.79
Stocking Density	2	755.05	11.49	0	751.05
Grazing System + Year	5	757.17	13.61	0	747.15
Null	1	758.94	15.38	0	756.94

Table 4. Support for candidate models predicting sharp-tailed grouse nest survival in 2016–18 within the rest-rotation system. Treatment represents whether the pasture was grazed during the growing season, post-growing season, or rested. The number of parameters (K), AIC_c values, ΔAIC_c , model weights (w_i) and deviance are reported.

Model	K	AIC_c	ΔAIC_c	$AIC_c w_i$	Deviance
Null	1	251.86	0	0.61	249.85
Stocking Rate	2	253.72	1.86	0.24	249.7
Treatment	3	255.42	3.57	0.1	249.4
Treatment + Stocking Rate	4	257.43	5.58	0.04	249.39
Treatment x Stocking Rate	6	261.46	9.61	0.01	249.39

Table 5. Sharp-tailed grouse brood survival (\pm SE) to fledging at 14-d post hatch for broods that spent the majority of time in pastures managed with each grazing system in 2016-2018. Brood success is the proportion of broods that successfully fledged ≥ 1 chick. Fledging rate is the proportion of chicks within broods that survived to fledging at 14 days.

	Number of Broods	Brood Success	Fledging Rate
Rest-rotation	22	0.59 \pm 0.10	0.55 \pm 0.08
Summer rotation	30	0.80 \pm 0.07	0.54 \pm 0.06
Season-long	29	0.66 \pm 0.09	0.59 \pm 0.07
Multiple systems	14	0.43 \pm 0.13	0.32 \pm 0.09
Total	95	0.65 \pm 0.05	0.54 \pm 0.4

Table 6. Estimated demographic rates (\pm SE) for female sharp-tailed grouse during the 2016–18 breeding seasons.

Demographic Rate	Estimate \pm SE
Nesting rate (NEST)	1
Clutch size - first nest (CS1)	11.06 \pm 0.57
Clutch size - renests (CS2)	9.57 \pm 0.60
Nest survival (NSURV)	0.40 \pm 0.04
Renesting rate (RENEST)	0.61 \pm 0.10
Chicks per egg laid (CPE)	0.91 \pm 0.02
Brood survival (BSURV)	0.69 \pm 0.05
Fledglings per chick hatched (FPC)	0.62 \pm 0.06

Table 7. Model selection results for Cox proportional hazards models evaluating both breeding season and non-breeding season survival of female sharp-tailed grouse during 2016–2018. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and log-likelihoods are reported. The % rest-rotation and % summer rotation variables represent the percent of a female’s 50% kernel home range composed of each grazing system.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. w_i	LL
<u>Breeding season</u>						
Null	1	997.04	0.00	0.48	0.48	-498.52
Year	5	998.99	1.95	0.18	0.66	-494.32
Female age	1	999.03	1.99	0.18	0.83	-498.50
% Summer rotation	3	1001.35	4.31	0.06	0.89	-497.60
% Summer rotation + Year	7	1001.57	4.54	0.05	0.94	-493.45
% Rest-rotation	3	1002.39	5.35	0.03	0.97	-498.12
% Rest-rotation + Year	7	1002.58	5.55	0.03	1.00	-493.95
<u>Non-breeding season</u>						
Year	2	383.89	0.00	0.90	0.90	-189.89
Null	1	388.94	5.05	0.07	0.97	-194.47
Female age	1	390.97	7.08	0.03	1.00	-194.47

Table 8. Model selection results for Andersen-Gill models of mortality risk in relation to landscape characteristics related to rangeland management and anthropogenic disturbance for female sharp-tailed grouse in eastern Montana and western North Dakota. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and log-likelihoods are reported. Edge density (ED) is defined as the total landcover edge length / polygon area.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. w_i	LL
Cropland	1	409.35	0.00	0.20	0.20	-203.68
Null	1	410.51	1.15	0.11	0.31	-205.25
Cropland + ED	2	410.62	1.27	0.11	0.42	-203.31
Stocking rate (prv. yr) + Cropland	2	410.65	1.30	0.10	0.52	-203.33
ED	1	410.97	1.62	0.09	0.61	-204.49
Stocking rate (cur. yr) + Cropland	2	411.33	1.98	0.07	0.68	-203.66
Stocking rate (prv. yr)	1	412.05	2.70	0.05	0.73	-205.03
Brood-rearing	1	412.10	2.75	0.05	0.78	-205.05
Stocking rate (prv. yr) + ED	2	412.36	3.01	0.04	0.83	-204.18
Stocking rate (cur. yr)	1	412.46	3.11	0.04	0.87	-205.23
Stocking rate (cur. yr) + ED	2	412.96	3.61	0.03	0.90	-204.48
Stocking rate (prv. yr) + Brood- rearing	2	413.62	4.27	0.02	0.93	-204.81

Stocking rate (cur. yr) + Stocking rate (prv. yr)	2	413.81	4.46	0.02	0.95	-204.90
Stocking rate (cur. yr) + Brood-rearing	2	414.05	4.70	0.02	0.97	-205.03
Stocking rate (prv. yr) x Brood-rearing	3	415.21	5.86	0.01	0.98	-204.60
Stocking rate (cur. yr) x Brood-rearing	3	415.94	6.58	0.01	0.99	-204.97
Grazing system + Cropland	5	417.14	7.79	0.00	0.99	-203.56
Grazing system	4	417.66	8.31	0.00	0.99	-204.83
Grazing system + ED	5	418.21	8.86	0.00	0.99	-204.10
Grazing system + Stocking rate (prv. yr)	5	418.91	9.55	0.00	1.00	-204.45
Grazing system + Brood-rearing	5	419.27	9.92	0.00	1.00	-204.63
Grazing system + Stocking rate (cur. yr)	5	419.59	10.24	0.00	1.00	-204.79
Grazing system + Stocking rate (prv. yr) + Stocking rate (cur. yr)	6	420.41	11.06	0.00	1.00	-204.20
Grazing system x Brood-rearing	9	425.81	16.46	0.00	1.00	-203.89

Table 9. Home range size (95% volume contour) for radio-marked female sharp-tailed grouse monitored in the 3 grazing systems during the breeding seasons of 2016–2018. Females were assigned to the grazing system containing $\geq 60\%$ of their home range or were considered to use multiple systems if no one system accounted for $\geq 60\%$ of their home range.

Grazing System	# Females	Mean area (ha) \pm	Min. area (ha)	Max area (ha)
		SE		
Rest-rotation	47	557 \pm 94	63.81	3717.45
Summer rotation	44	361 \pm 39	86.13	1198.89
Season-long	36	408 \pm 43	57.51	1103.58
Multiple systems	15	838 \pm 179	191.43	2265.66
Total	142	489 \pm 41	57.51	3717.45

Table 10. Support for candidate models predicting the home range size of female sharp-tailed grouse during the breeding seasons of 2016–2018. The percent of a home range containing either the rest-rotation or summer rotation system are measured in relation to the season-long system. The number of parameters (K), AIC_c values, Δ AIC_c values, model weights (w_i), and log-likelihoods are reported.

Model	K	AIC _c	Δ AIC _c	AIC _c w_i	Cum. w_i	LogLik
Edge density	3	2157.27	0.00	0.93	0.93	-1075.55
Dist. to grassland edge	3	2165.05	7.78	0.02	0.95	-1079.44
Nest outcome	3	2165.25	7.98	0.02	0.96	-1079.54
Null	2	2166.80	9.53	0.01	0.97	-1081.36

Year	3	2167.47	10.20	0.01	0.98	-1080.65
% Rest-rotation	3	2167.71	10.43	0.01	0.98	-1080.77
Stocking rate	3	2168.12	10.84	0.00	0.99	-1080.97
% Summer rotation	3	2168.14	10.87	0.00	0.99	-1080.98
Dist. to lek	3	2168.65	11.38	0.00	0.99	-1081.24
Dist. to road	3	2168.73	11.46	0.00	0.99	-1081.28
Dist. to oil pad	3	2168.84	11.57	0.00	1.00	-1081.33
Prop. grassland	3	2168.88	11.61	0.00	1.00	-1081.36

Table 11. Simplified ranking matrix of female sharp-tailed grouse breeding season habitat selection based on vegetation type in 2016-2018. Matrix is based on comparing proportional habitat use within home ranges with the proportion of available habitat types. The ‘other’ habitat is composed primarily of ruderal grasslands. Habitat types with the same rank suggest that females did not differentiate between the two categories in habitat selection.

	Grassland	Wooded draws	Other	Agriculture	RANK
Grassland	0	+	+++	+++	1
Wooded draws	-	0	+++	+++	1
Other	---	---	0	+++	3
Agriculture	---	---	---	0	4

Table 12. Support for final candidate models evaluating sharp-tailed grouse nest site selection in 2016–18 in the three analyses examining habitat-level variables, management-level variables, and the combined analysis. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and log-likelihoods are reported. VOR is visual obstruction as measured at the nest bowl and mean shape complexity (MSI) is a measure of patch shape irregularity and is defined as the sum of each landcover patch’s perimeter divided by the square root of each patch area and divided by the number of patches, such that it equals 1 when all patches are circular.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. w_i	LogLik
<u>Habitat Analysis</u>						
ln(VOR) + %Residual + Mean Shape Complexity	5	284.95	0.00	0.61	0.61	-137.40
ln(VOR) + %Grass + %Residual + %Shrub + Mean Shape Complexity	7	285.97	1.02	0.37	0.98	-135.83
ln(VOR) + %Grass + %Residual + %Shrub	6	293.20	8.25	0.01	0.99	-140.49
ln(VOR) + %Residual	4	294.22	9.27	0.01	1.00	-143.06
Mean Shape Complexity	3	524.93	239.97	0.00	1.00	-259.43
Null	2	528.04	243.09	0.00	1.00	-262.00
<u>Management Analysis</u>						
Stocking Rate (prv. yr)	3	526.45	0.00	0.26	0.26	-260.19

Stocking Rate (prv. yr) + Grazing System	5	526.54	0.09	0.25	0.51	-258.19
Null	2	528.04	1.59	0.12	0.63	-262.00
Stocking Rate (cur. yr)	3	528.49	2.05	0.09	0.73	-261.22
Grazing System	4	528.90	2.45	0.08	0.81	-260.40
Stocking Rate (cur. yr) * Grazing System	7	529.71	3.26	0.05	0.86	-257.70
Stocking Rate (cur. yr) + Grazing System	5	529.85	3.40	0.05	0.90	-259.85
Grazing System * Stocking Rate (prv. yr)	7	530.34	3.89	0.04	0.94	-258.02
Stocking Rate (prv. yr) + Year	5	530.51	4.06	0.03	0.98	-260.17
Stocking Rate (cur. yr) + Year	5	532.47	6.02	0.01	0.99	-261.16
Grazing System + Year	6	533.02	6.57	0.01	1.00	-260.40
Grazing System * Year	10	541.07	14.62	0.00	1.00	-260.24

Full Analysis

ln(VOR) + %Residual + MSI	5	284.95	0.00	0.58	0.58	-137.40
ln(VOR) + %Residual + MSI + Stocking Rate (prv. yr.)	6	285.57	0.61	0.42	1.00	-136.67
Stocking Rate (prv. yr.)	3	526.45	241.49	0.00	1.00	-260.19
Null	2	528.04	243.09	0.00	1.00	-262.00

Table 13. Estimates and 95% credible intervals for fecundity parameters in 2016 from a female-based integrated population model on Sharp-tailed grouse in western Montana.

age class:	yearling		adult	
	est	95% CI	est	95% CI
clutch size, first nest	12.18	(11.364, 13.027)	12.57	(11.734, 13.44)

clutch size, second nest	9.33	(7.826, 10.871)	8.62	(7.378, 9.907)
hatchability	0.92	(0.892, 0.947)	0.91	(0.881, 0.941)
nest propensity, second nest	0.56	(0.359, 0.757)	0.60	(0.41, 0.78)
recruitment	0.27	(0.163, 0.4)	0.23	(0.137, 0.352)
annual survival	0.45	(0.614, 0.807)	0.62	(0.501, 0.724)
breeding season survival	0.72	(0.716, 0.807)	0.82	(0.75, 0.874)
chick survival	0.21	(0.156, 0.269)	0.18	(0.132, 0.238)
nest survival, first nest	0.45	(0.223, 0.668)	0.36	(0.138, 0.594)
nest survival, second nest	0.75	(0.258, 0.992)	0.83	(0.438, 0.996)

Table 14. Estimates and 95% credible intervals for fecundity parameters in 2017 from a female-based integrated population model on Sharp-tailed grouse in western Montana.

parameter	yearling		adult	
	est	95% CI	est	95% CI
clutch size, first nest	11.80	(10.923, 12.716)	12.18	(11.305, 13.072)
clutch size, second nest	10.14	(8.587, 11.978)	9.38	(7.831, 11.346)
hatchability	0.91	(0.874, 0.939)	0.90	(0.87, 0.928)
nest propensity, second nest	0.48	(0.28, 0.679)	0.52	(0.337, 0.689)
recruitment	0.29	(0.183, 0.408)	0.25	(0.16, 0.356)
annual survival	0.38	(0.229, 0.539)	0.56	(0.434, 0.669)
breeding season survival	0.67	(0.541, 0.773)	0.78	(0.706, 0.845)
chick survival	0.22	(0.174, 0.267)	0.19	(0.148, 0.235)
nest survival, first nest	0.52	(0.293, 0.73)	0.43	(0.231, 0.643)
nest survival, second nest	0.75	(0.241, 0.991)	0.82	(0.437, 0.996)

Table 15. Estimates and 95% credible intervals for fecundity parameters in 2018 from a female-based integrated population model on Sharp-tailed grouse in western Montana.

parameter	yearling		adult	
	est	95% CI	est	95% CI
clutch size, first nest	11.35	(10.333, 12.395)	11.71	(10.72, 12.721)
clutch size, second nest	9.89	(8.146, 11.919)	9.14	(7.66, 10.857)
hatchability	0.93	(0.899, 0.952)	0.92	(0.891, 0.946)
nest propensity, second nest	0.50	(0.272, 0.711)	0.53	(0.318, 0.731)
recruitment	0.39	(0.249, 0.545)	0.35	(0.22, 0.498)
annual survival	0.48	(0.313, 0.654)	0.64	(0.517, 0.758)
breeding season survival	0.74	(0.616, 0.838)	0.83	(0.759, 0.891)
chick survival	0.27	(0.21, 0.34)	0.24	(0.18, 0.303)
nest survival, first nest	0.64	(0.415, 0.821)	0.56	(0.342, 0.763)
nest survival, second nest	0.67	(0.034, 0.992)	0.76	(0.164, 0.996)

Table 16. Hazard ratios for effects of grazing system on key vital rates of Sharp-tailed grouse estimated with a Bayesian hierarchical integrated population model. Season-long grazing is the reference category. Field data was collected in western Montana from 2016-2018. Hazard ratios and 95% credible intervals suggest that on average grazing system does not differentially or significantly impact nest survival, chick survival, or annual survival of adult, female grouse.

parameter	grazing system			
	<u>rest-rotation</u>		<u>summer rotation</u>	
	est	95% CI	est	95% CI
ln(hazard ratio), second nest survival	0.02	(-0.324, 0.367)	0.30	(0.003, 0.597)
ln(hazard ratio), first nest survival	0.14	(-0.503, 0.802)	0.36	(-0.285, 1.026)
ln(hazard ratio), chick survival	0.90	(-1.482, 3.832)	1.51	(-0.728, 4.653)
ln(hazard ratio), adult survival	0.32	(-0.101, 0.744)	0.64	(0.211, 1.064)
hazard ratio, second nest survival	1.02	(0.723, 1.443)	1.35	(1.003, 1.816)
hazard ratio, first nest survival	1.15	(0.604, 2.229)	1.43	(0.752, 2.789)
hazard ratio, chick survival	2.45	(0.227, 46.154)	4.51	(0.482, 104.899)
hazard ratio, adult survival	1.38	(0.903, 2.104)	1.89	(1.234, 2.897)

Table 17. Posterior mean estimates and 95% credible intervals of lambda, female population size, intrinsic rate of growth (r) and juvenile survival (from informative prior) for an integrated population model on Sharp-tailed grouse using field data collected from 2016 to 2018.

parameter	year	est	95% CI		Rhat
			LL	UL	
juvenile survival		0.402	0.343	0.464	1.000
lambda	2016 to 2017	0.741	0.615	0.874	1.001
lambda	2017 to 2018	0.686	0.535	0.837	1.001
pop. size	2016	264	226	299	1.001
pop. size	2017	195	156	231	1.001
pop. size	2018	134	95	171	1.001
r	2016 to 2017	-0.303	-0.485	-0.134	1.001
r	2017 to 2018	-0.381	-0.624	-0.177	1.001

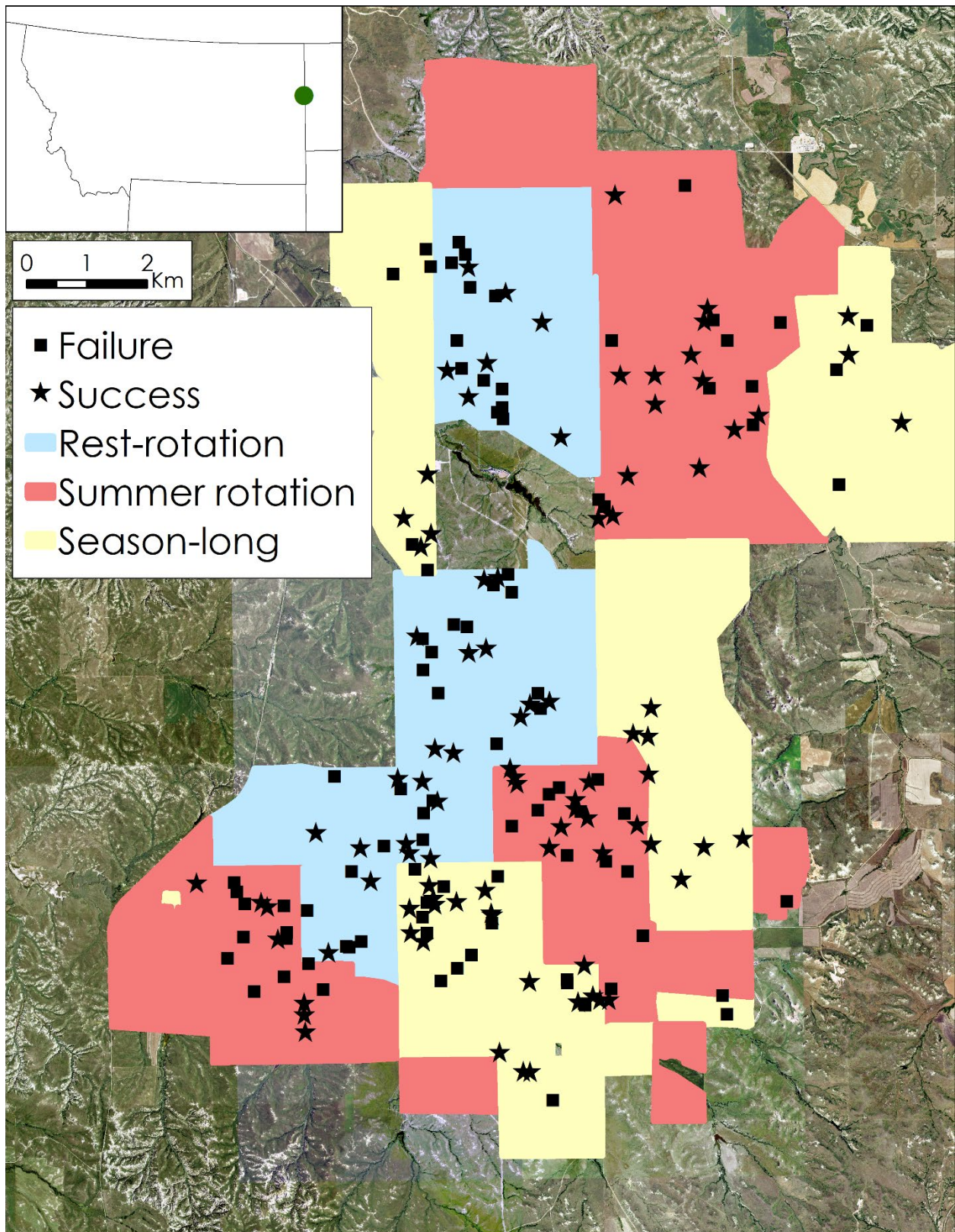


Figure 1. Locations of successful (stars) and failed (squares) sharp-tailed grouse nests in 2016–18 in relation to different grazing treatments.

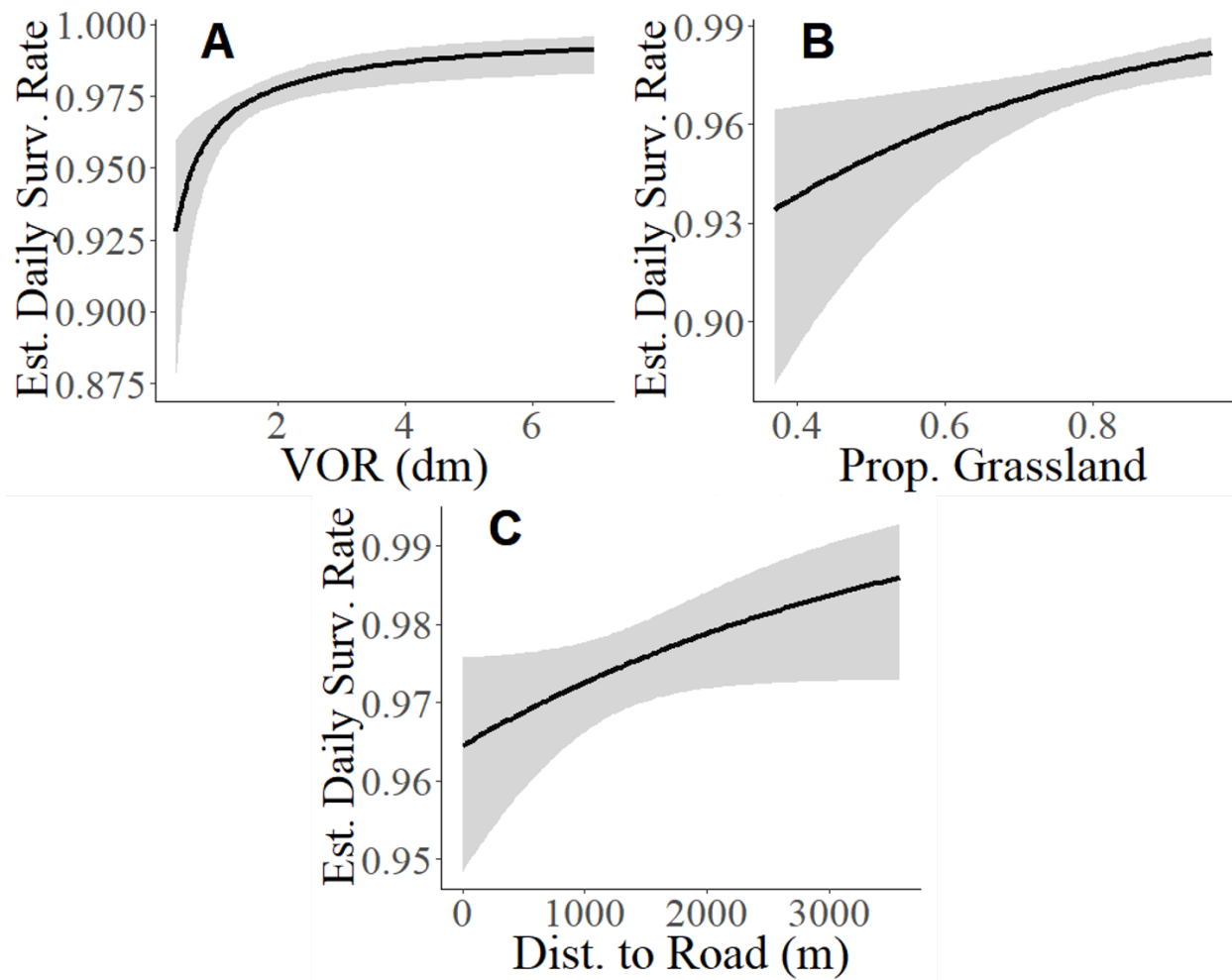


Figure 2. Estimated daily nest survival in relation to important habitat variables, with 85% confidence intervals shown in grey. Visual obstruction (VOR) was averaged across the 6 m vegetation plot.

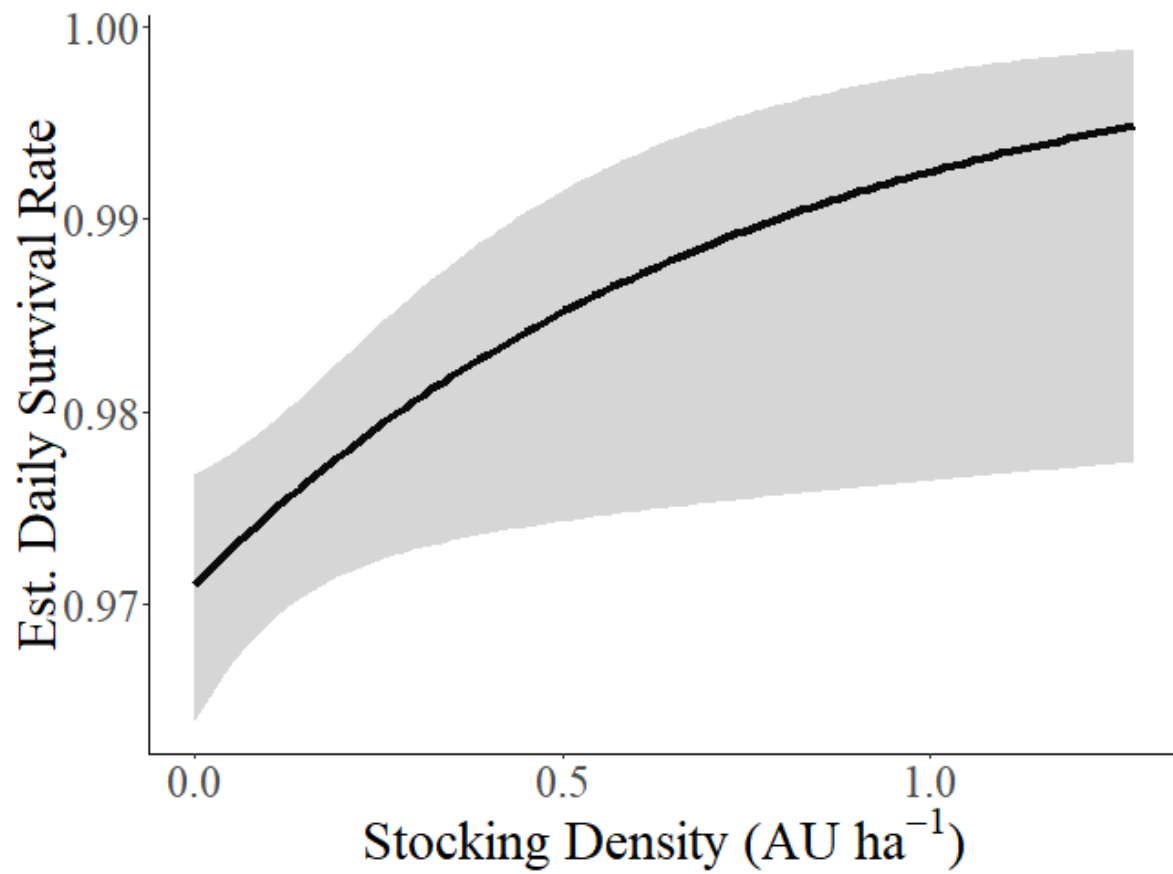


Figure 3. Estimated daily nest survival in relation to stocking density while the nest was active, with 85% confidence intervals shown in grey.

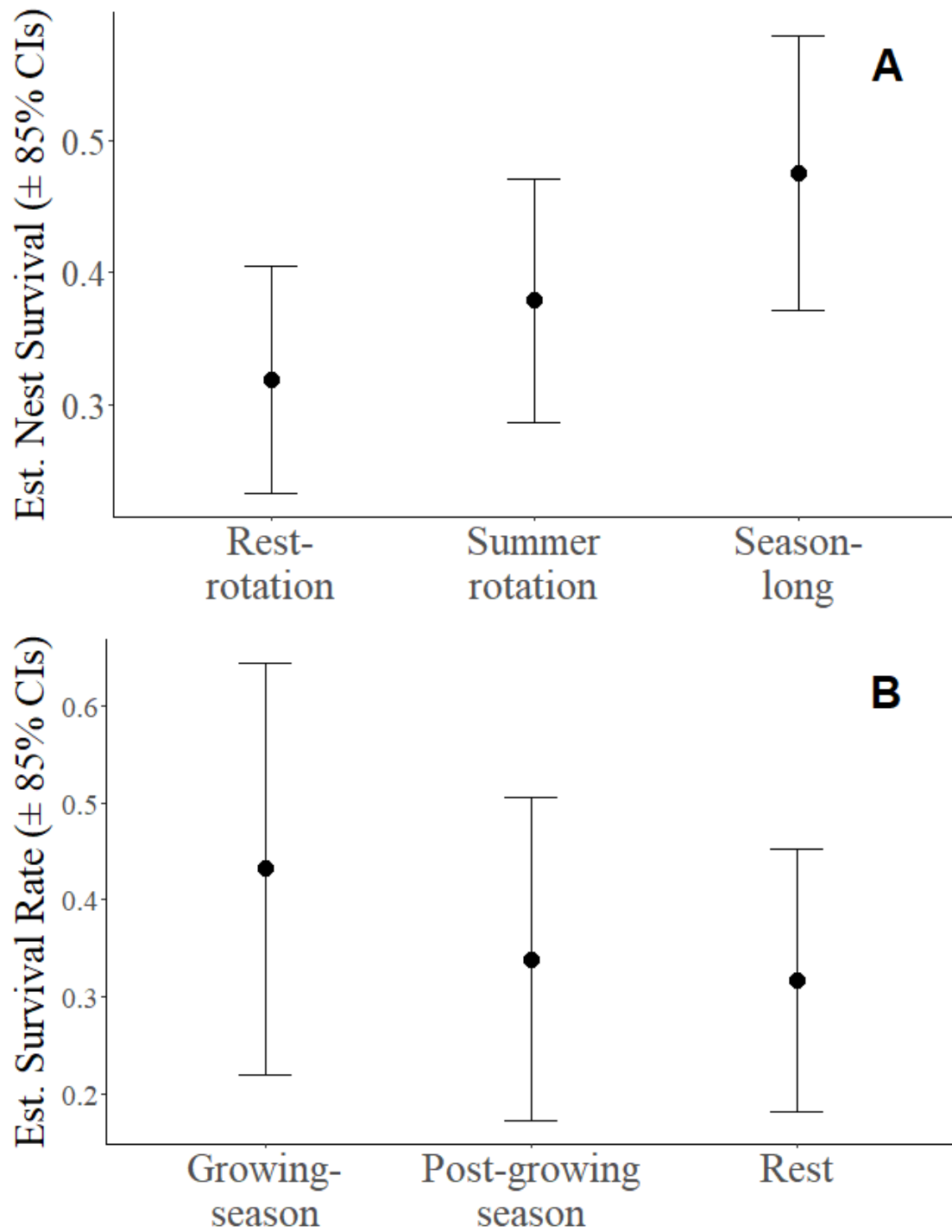


Figure 4. Estimated overall nest survival (\pm 85% confidence intervals) for sharp-tailed grouse in each of the three grazing treatments (A) and in each of the three treatments within the rest-rotation system in 2016–18 (B).

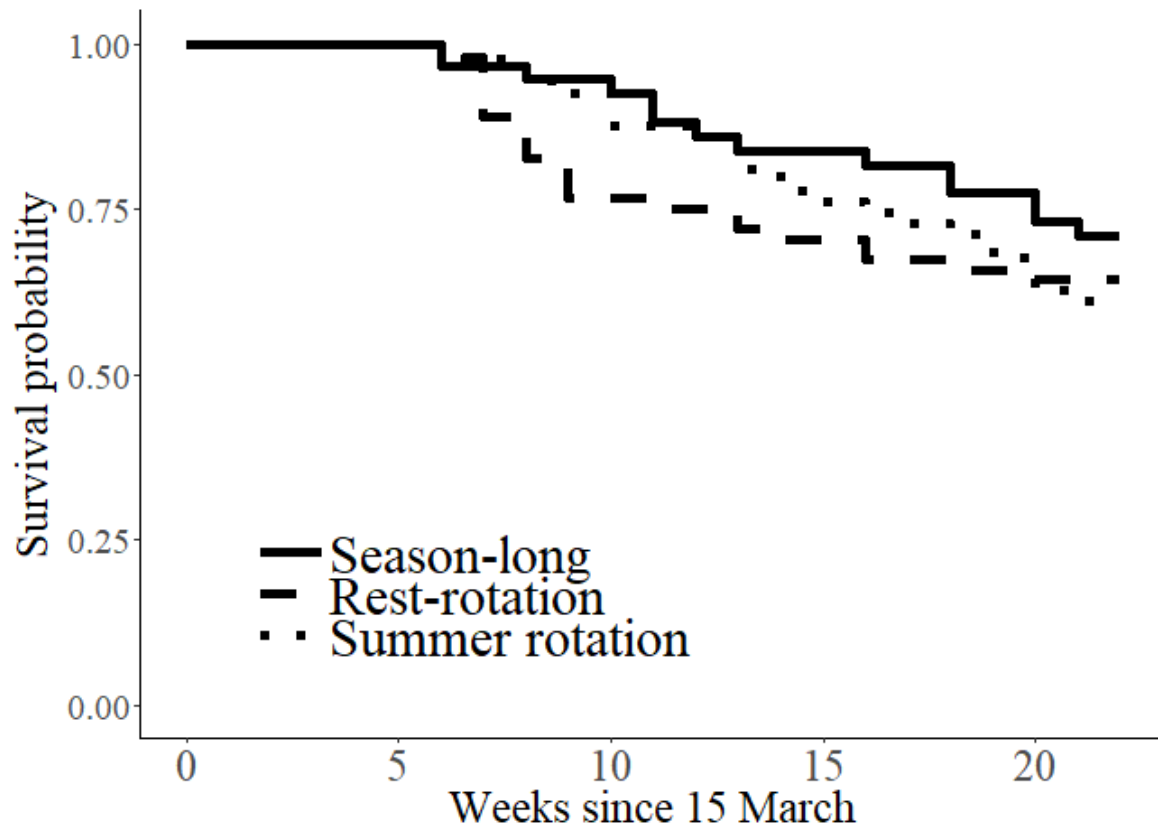


Figure 5. Kaplan-Meier plot of cumulative weekly survival during the breeding season of radio-marked female sharp-tailed grouse associated with 3 grazing systems in eastern Montana and western North Dakota. Confidence intervals omitted for clarity.

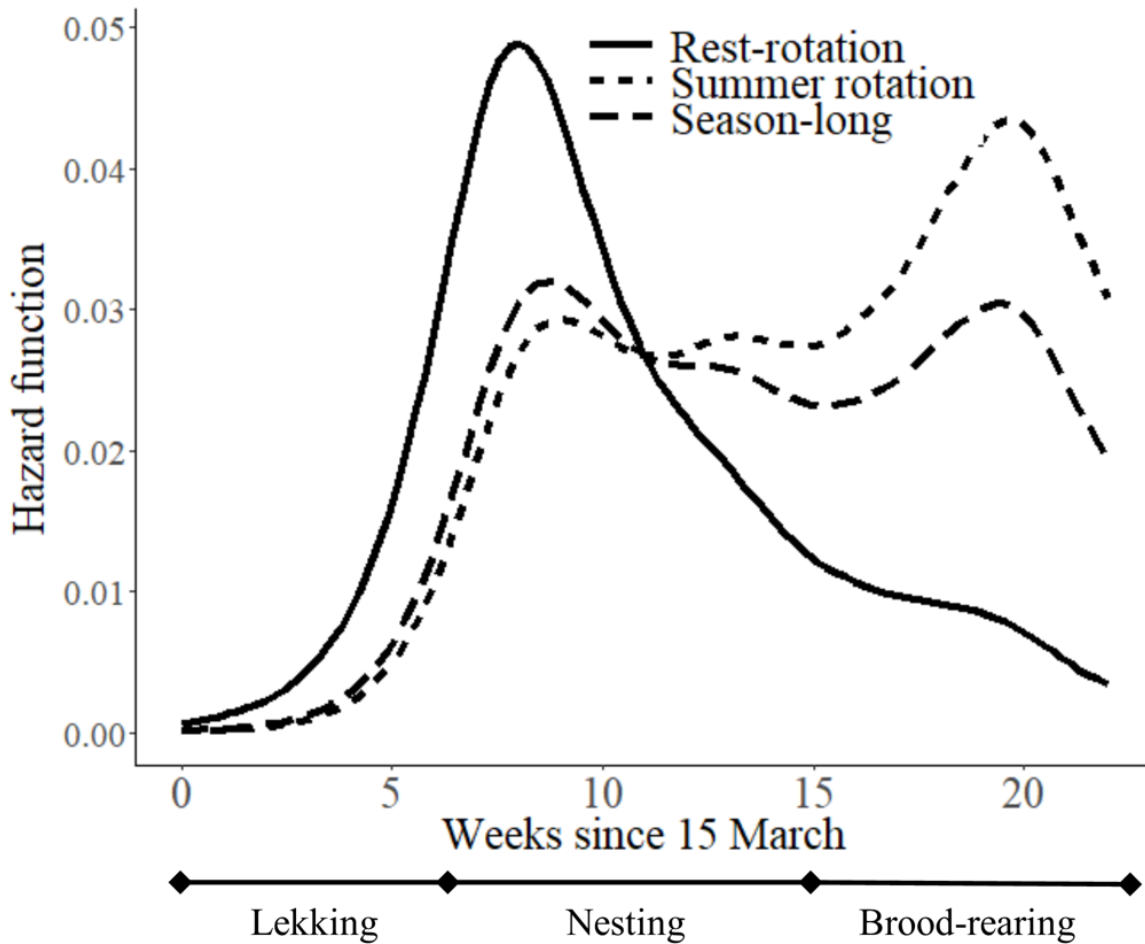


Figure 6. Weekly hazard functions during the breeding season for female sharp-tailed grouse associated with 3 grazing systems in eastern Montana and western North Dakota. Confidence intervals omitted for clarity. The approximate timing of lekking, nesting and brood-rearing activity is shown at the bottom.

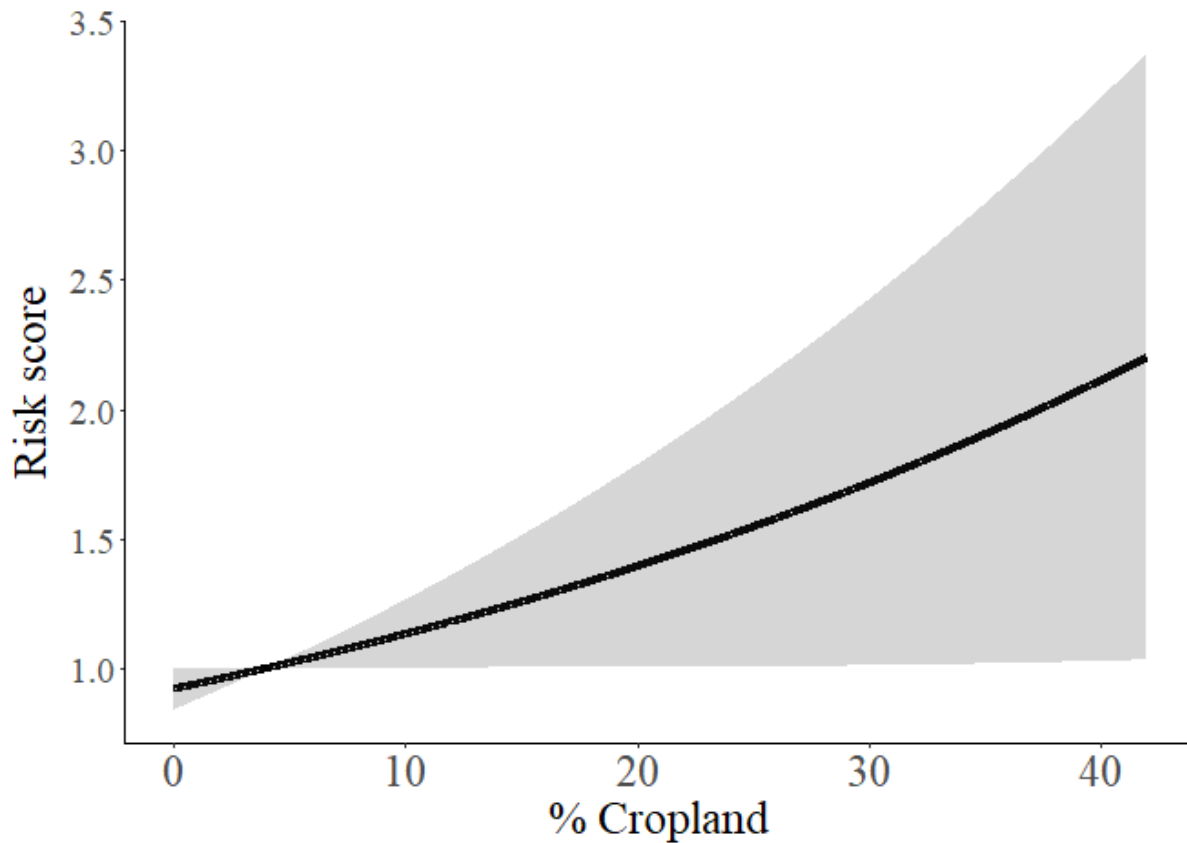


Figure 7. Risk score (\pm 85% confidence intervals) from an Andersen-Gill formulation of the Cox proportional hazards model estimating the risk of mortality for female sharp-tailed grouse relative to the percent agriculture within 1,300 m in eastern Montana and western North Dakota.

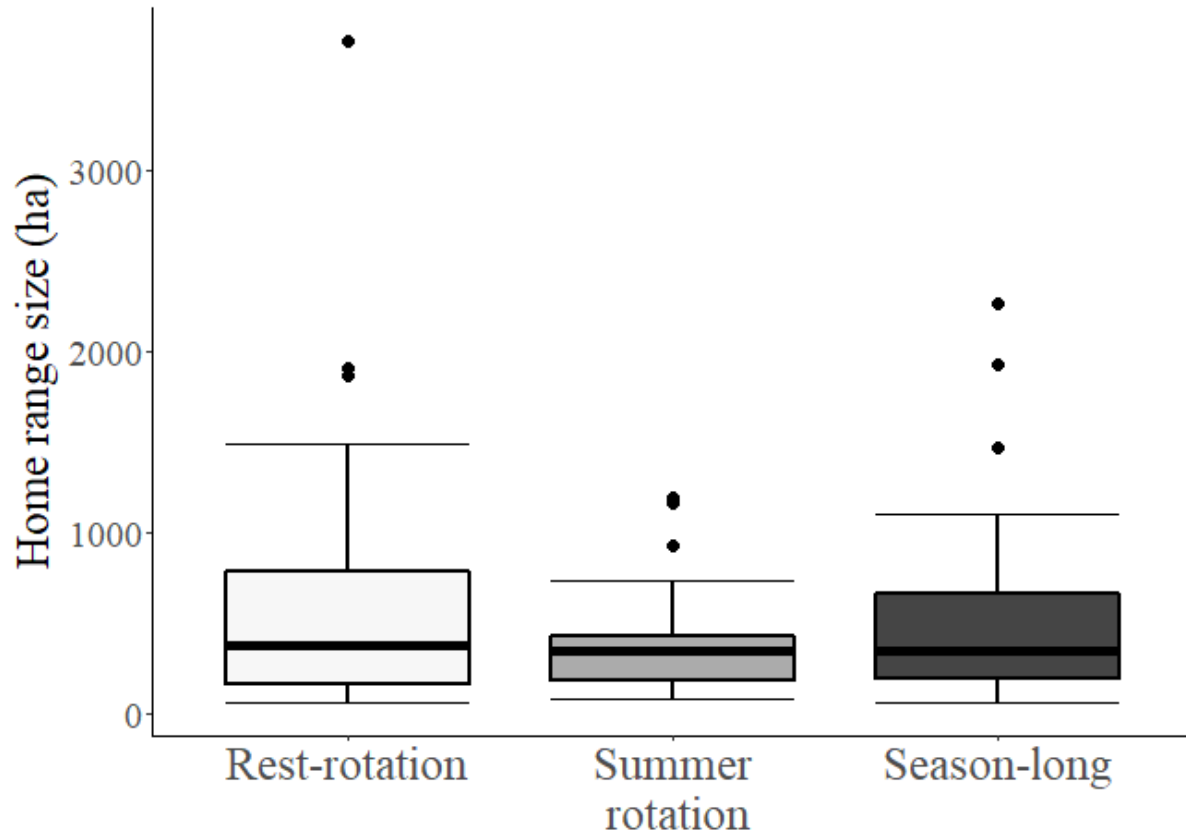


Figure 8. Female sharp-tailed grouse breeding season home range size (\pm SE) by grazing system. An individual female was assigned to a grazing system according to the system containing \geq 60% of the individual's home range.

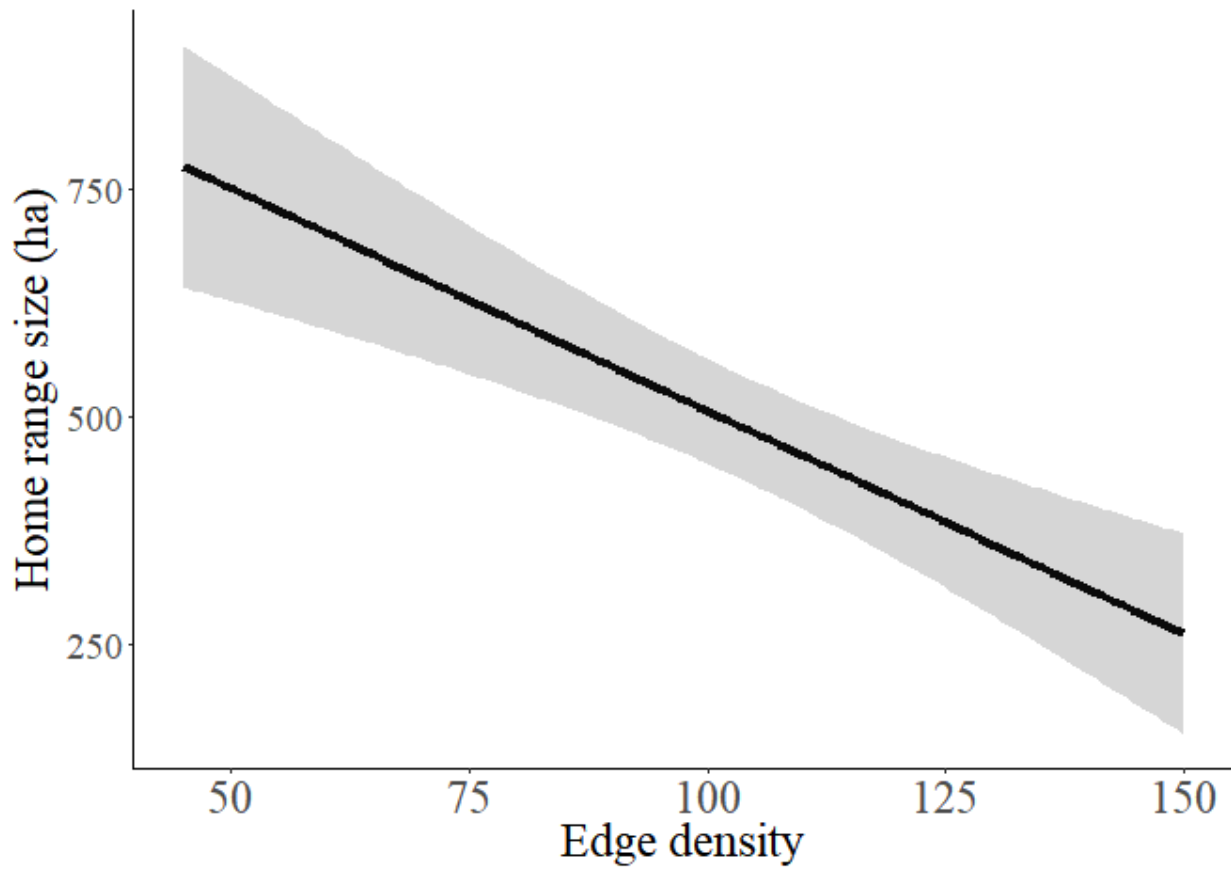


Figure 9. Relationship (\pm 85% confidence intervals) between the density of edge habitat (total landcover edge length / polygon area) and breeding season home range size for female sharp-tailed grouse.

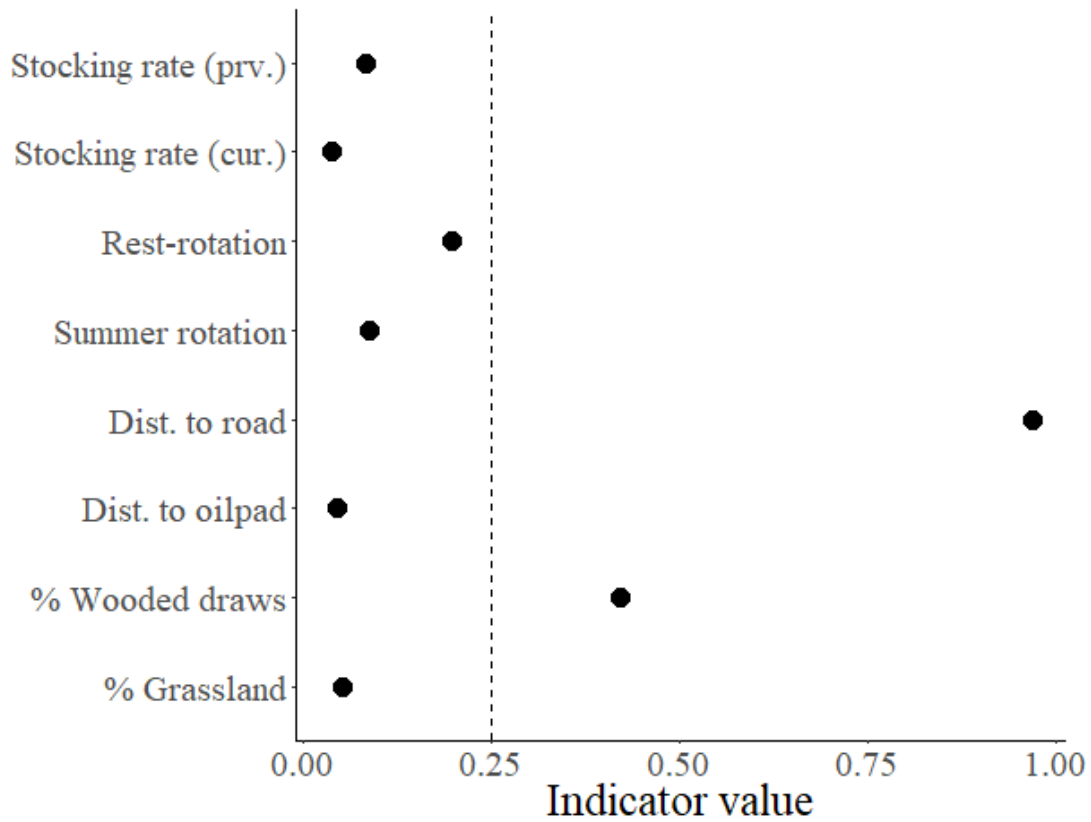


Figure 10. Bayesian variable selection identifying important predictors of sharp-tailed grouse third-order habitat selection during the breeding season. Predictors with indicator variables ≤ 0.25 are considered unimportant.

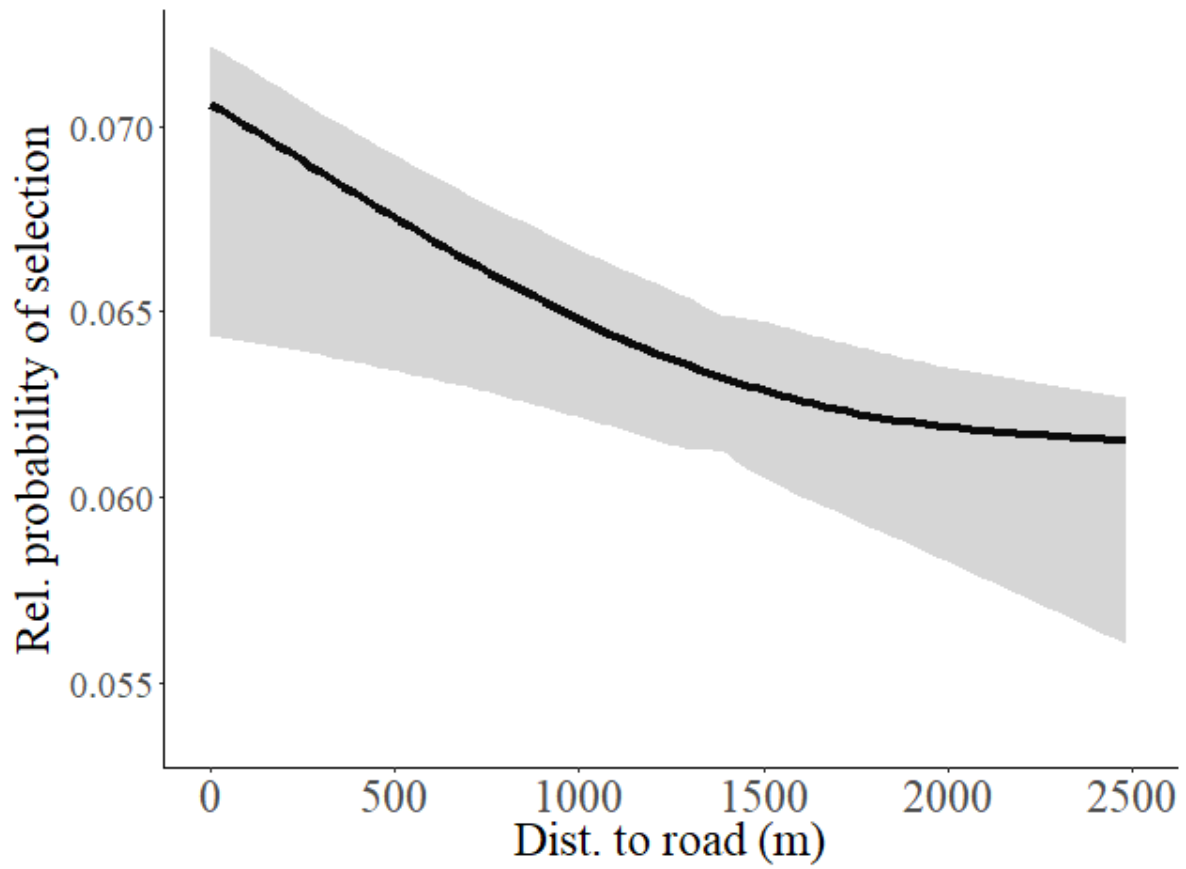


Figure 11. Relationship (\pm 95% credible intervals) between the distance to a road and the relative probability of selection of female sharp-tailed grouse within the breeding season home range.

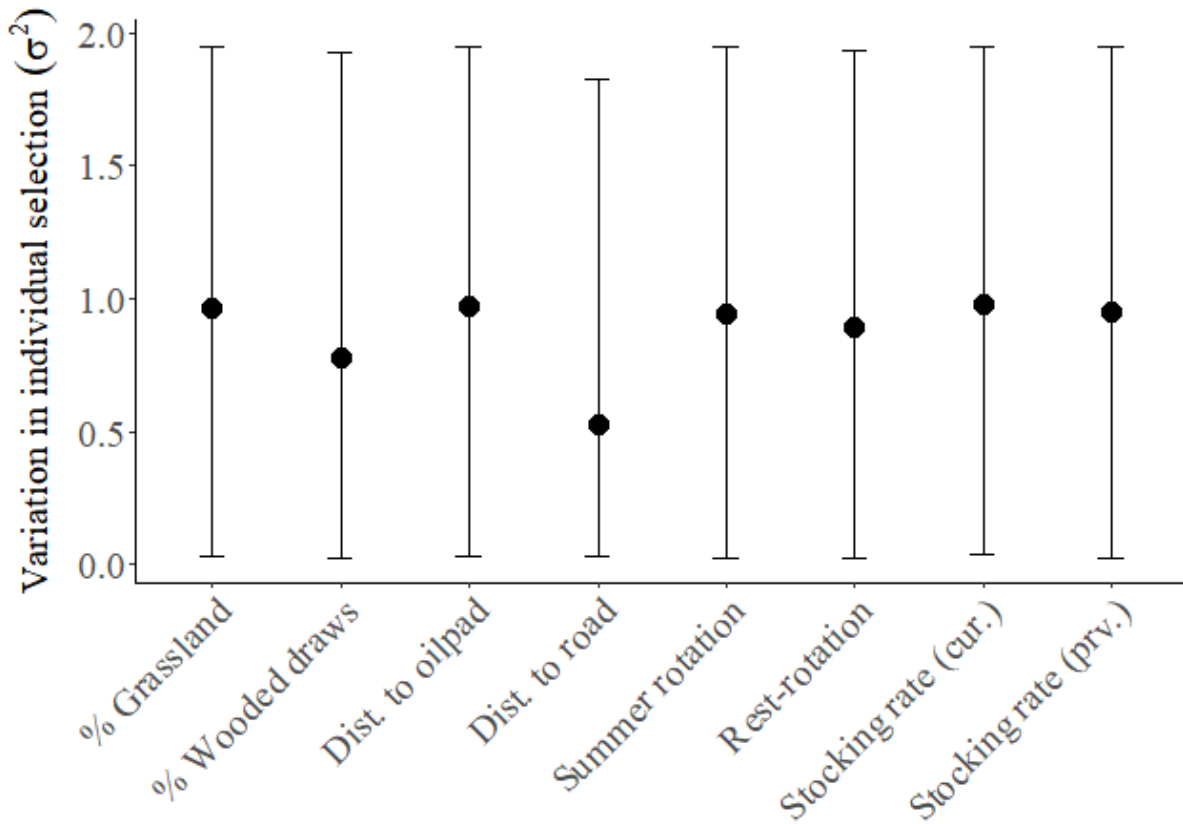


Figure 12. Posterior estimates of the variability in selection ($\sigma^2 \pm 95\%$ credible intervals) among individual female sharp-tailed grouse for each habitat variable. σ^2 is a measure of how strongly individuals varied in selection for different habitat variables. Habitat variables were scaled prior to model fitting.

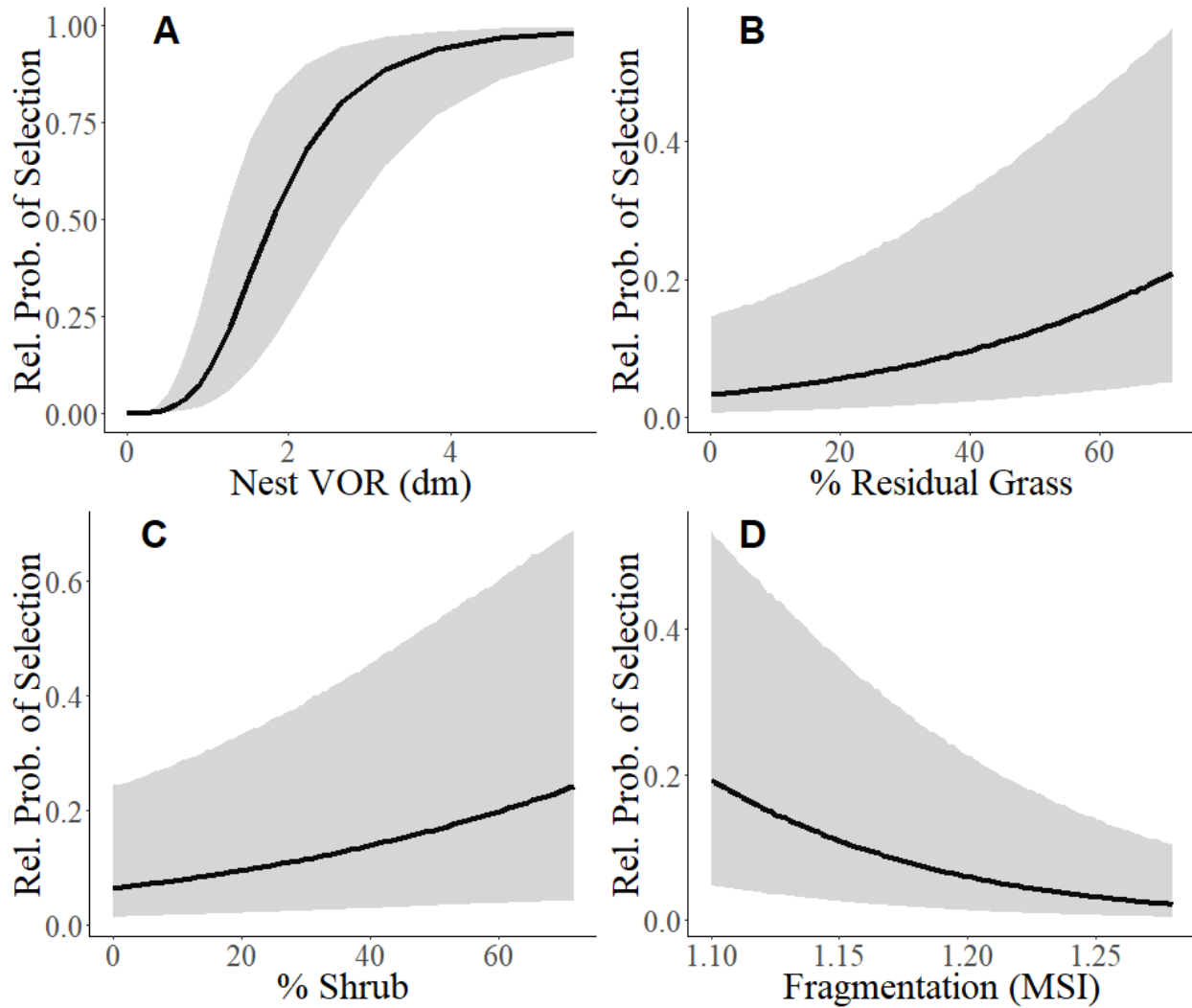


Figure 13. Estimated relative probability of nest site selection in relation to important habitat variables, with 85% confidence intervals shown in grey. Visual obstruction (VOR) was measured at the nest bowl.

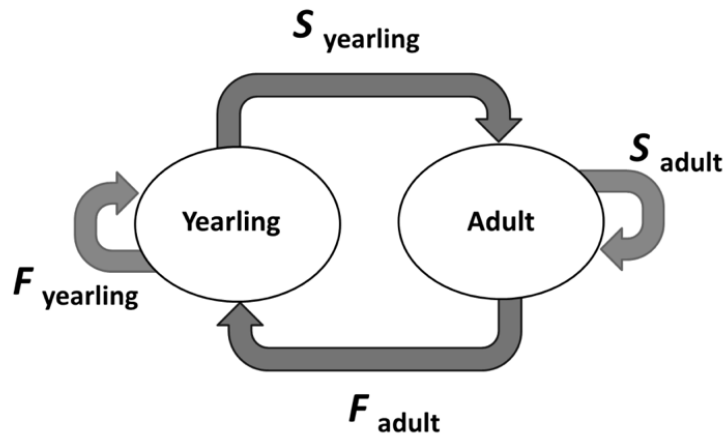


Figure 14. A two-stage conceptual model from Coates et al. 2014 depicting the life history of grouse, with nodes being yearling and adult bird stage classes. F represents contributions to the population of fecundity and S represents survival.