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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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FINAL PERFORMANCE REPORT

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EXECUTIVE SUMMARY

This report summarizes the results of a 4-year field study 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 were 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 meso-predators. Our study site was located in eastern Montana on properties enrolled in the Upland Game Bird Enhancement Program and adjacent properties not enrolled in conservation programs with prescriptive grazing. Field work was conducted during 2016–2019 and final analyses completed during 2020–2021. In this report we present study results for all original project objectives, including those completed during preceding years, as well as additional objectives.

1. We addressed seven potential effects of grazing management and habitat conditions on sharp-tailed grouse: nest site selection, nest survival, breeding season home ranges and habitat selection, brood habitat selection, adult female survival, and population growth and viability. Our monitoring efforts during the 4-year study period included 12 leks, 118 radio-marked females monitored for 180 bird-years, 7,178 individual locations of radio-marked females, 188 nesting attempts, and 95 broods that were monitored until they failed or reached independence at 60 days.

    1.1. *Nest site selection and survival* – We located 188 grouse nests (147 first nests, 41 renesting attempts) laid by 128 individual females during 2016–2018. We evaluated nest site selection using resource selection functions calibrated with generalized linear mixed models. Nest site selection was not affected by grazing system. Instead, females selected nest sites in areas with high grassland contagion and nest site selection was best predicted by local visual obstruction (VOR; and index of nest concealment) and the percentage of new grass, residual grass, and shrubs. Nest survival varied by year and ranged from 0.29 ± 0.06 in 2016 to 0.48 ± 0.07 in 2018. We evaluated the effects of habitat conditions and management at two spatial scales. At the home-range scale, daily nest survival was negatively related to proximity to roads and positively related to proportion of the home range classified as grassland. At the nest site scale (within 6 m of a nest), nest survival was largely determined by VOR. Daily nest survival increased with proportion grassland ($\beta = 0.16 \pm 0.10$), distance to road ($\beta = 0.21 \pm 0.11$), and VOR up to a threshold of 20–30 cm, as represented by the pseudo-threshold model ($\beta = 0.29 \pm 0.11$). Grazing system did not influence nest site selection or nest survival. 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. Estimates of overall nest survival in the three treatments overlapped entirely.

    1.2. *Breeding season home ranges and habitat selection* – Mean breeding season home range size for 118 females was 489 ± 41 ha but varied from 58–3,717 ha. Home range sizes were less variable within pastures managed with summer rotation grazing compared to

those in other systems, but grazing system did not have a significant effect on average size of home ranges. Density of edge habitat within the home range was negatively related to the size of breeding season home ranges. 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. We found no evidence that grazing system affected breeding season habitat selection of home ranges. Within home ranges, females selected for areas farther from roads (β = -0.047 ± 0.001SE). In general, individual variability in habitat selection was high.

1.3. *Brood success and habitat selection* – 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. Soil type influenced second-order selection of home ranges by brood-rearing females, whereas similarity index influenced third-order selection within home ranges. We could not confirm our hypothesis that differences in relative habitat selection among soil types resulted from differences in vegetation structure or functional group composition. Within home ranges, females selected for sites with a lower similarity index, which were generally associated with higher variability in fine-scale vegetation density (e.g., VOR) and forbs, and lower shrub cover.

1.4. *Adult 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%). Overall survival (± 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. 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). In contrast, non-breeding season survival differed among the 3 study years 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. Overall annual survival was similar for females who spent the majority of their time in the three grazing systems; however, we observed variability in seasonal mortality risk among the three systems. Mortality risk peaked in early May during the nesting period in all grazing systems, but 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.

1.5. *Population growth and viability* – 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 renesting attempts, clutch sizes of first and renests, hatchability of nests, nest survival of first and renests, 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 (λ = 0.69; 95%CrI: 0.54–0.84) resulting from depressed fecundity likely due to drought. We did not find support for cumulative effects of grazing system on population growth rates of sharp-tailed grouse; 95% credible intervals of rates of population change for each grazing system overlapped.

2. We investigated the effects of livestock grazing management on the abundance and diversity of grassland songbirds. We used 1,830 point-count surveys and N-mixture models to estimate the abundance and diversity of grassland birds in relation to three livestock grazing systems: rest rotation, within season rotational grazing, and continuous season-long grazing. In addition, we surveyed vegetation structure and composition at all bird survey locations.

2.1. *Local abundance* – We detected a total of 68 species of birds, 31 of which were grassland-associated species. In contrast to our expectations, rest-rotation grazing did not support greater local abundances of three native ground-nesting grassland obligate birds relative to summer-rotation or season-long grazing systems during our 2-year study, despite modest differences among grazing systems in vegetation composition and structure. Rather, associations among local abundance, grazing system, stocking rate, and rangeland production potential were species-specific and do not support ubiquitous grazing management recommendations for grassland bird conservation.

2.2. *Species richness and community composition* – We recorded 21 grassland-associated species in pastures within rest-rotation grazing systems, 24 species in two-pasture summer-rotation grazing systems, and 22 in season-long grazing systems. Grassland bird community size and composition was similar across the three grazing systems; only 2% of the variation in community composition could be attributed to the livestock grazing system.

3. We used camera traps to evaluate the effects of livestock grazing management and other habitat characteristics on mesocarnivore occupancy (i.e., relative use). We recorded 178 mesocarnivore detections during 3,535 camera trap days at 164 remote camera sites located within 8 pastures managed for cattle grazing. Relative use of mesocarnivores was highest in rest-rotation grazing systems, followed by season-long and summer-rotation grazing systems, and generally increased with stocking rates of livestock.

4. We contracted with Dr. Todd Cross and the USFS National Genomics Center for Wildlife and Fish Conservation to evaluate genetic diversity and pair-wise relatedness of female sharp-tailed grouse captured during the study. The per-locus number of alleles ranged from 2 to 27 (median = 13) and the population had observed levels of heterozygosity comparable to other prairie and sage-grouse populations in in-tact habitats (mean $H_O = 0.78 \pm 0.14$; expected mean heterozygosity ($\mathrm{H}_\mathrm{E} = 0.83 \pm 0.11$). The proportion of shared alleles (D_PS) varied from 0 to 0.96 indicating a full gradient of genetic relatedness among individuals in the study population.

5. We published the results of this study in six peer-reviewed scientific articles and have submitted an additional two that are currently in review at peer-reviewed journals (below). In addition, we published two graduate dissertations and two extension/outreach publications and gave 26 seminars/presentations at professional conferences, workshops, and agricultural outreach events. The project funded the training of two graduate students (1 Ph.D., 1 M.S.), one post-doctoral researcher, and 21 undergraduate field and laboratory technicians.

Published products († indicates graduate and undergraduate students; listed chronologically):

Vold. S.T.† and L.B. McNew. 2018. Effects of livestock grazing management on occupancy of mesocarnivores in a northern mixed-grass prairie ecosystem. Montana State University College of Agriculture and Extension Research Report 4:40–44.

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.

Milligan, M.C.†, and L.B. McNew. 2019. Effects of scavenging on assumptions of mortality analyses of radio-marked gamebirds. Northwestern Naturalist 100:197–205.

Milligan, M.C.† and L.B. McNew. 2019. Does cattle grazing affect nesting sharp-tailed grouse? Montana State University College of Agriculture and Extension Research Report 5.

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.

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. Survival of sharp-tailed grouse under variable livestock grazing management. Journal of Wildlife Management 84: 1296–1305.

Milligan, M.C.†, and L.B. McNew. 2021. Does researcher activity impact the nest survival of sharp-tailed grouse? Wildlife Biology, accepted 6/2021.

McNew, L., A. Lipinski, and M. Milligan†. *In review*. Evaluating the cumulative effects of livestock grazing on wildlife with an integrated population model. Submitted to Frontiers in Ecology and Evolution.

Macon, L.†, M. Milligan†, J. Mosley, and L.B. McNew. *In review*. Using ecological site condition to evaluate habitat selection by sharp-tailed grouse broods. Submitted to Rangeland Ecology and Management.

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OBJECTIVES

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

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.

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

Nesting rate (NEST) was calculated as the percentage of females that attempted a nest. The probability of renesting (RENEST) was calculated as the number of observed renesting attempts divided by the number of unsuccessful first nests minus the number of females that had first nests but were unavailable to renest. 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:

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

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 calculating 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 ≥ 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 (≥ 60%) of that individual's locations. Females for which one grazing system did not account for ≥ 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 (wi; Burnham and Anderson 2002). Parameters were considered uninformative if ΔAICc < 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, eβ), 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 (ΔAICc < 2 from best-fit model) and AICc weights ($\Sigma wi > 0.3$). Models that differed from the top model by a single parameter with ΔAICc < 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.

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

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

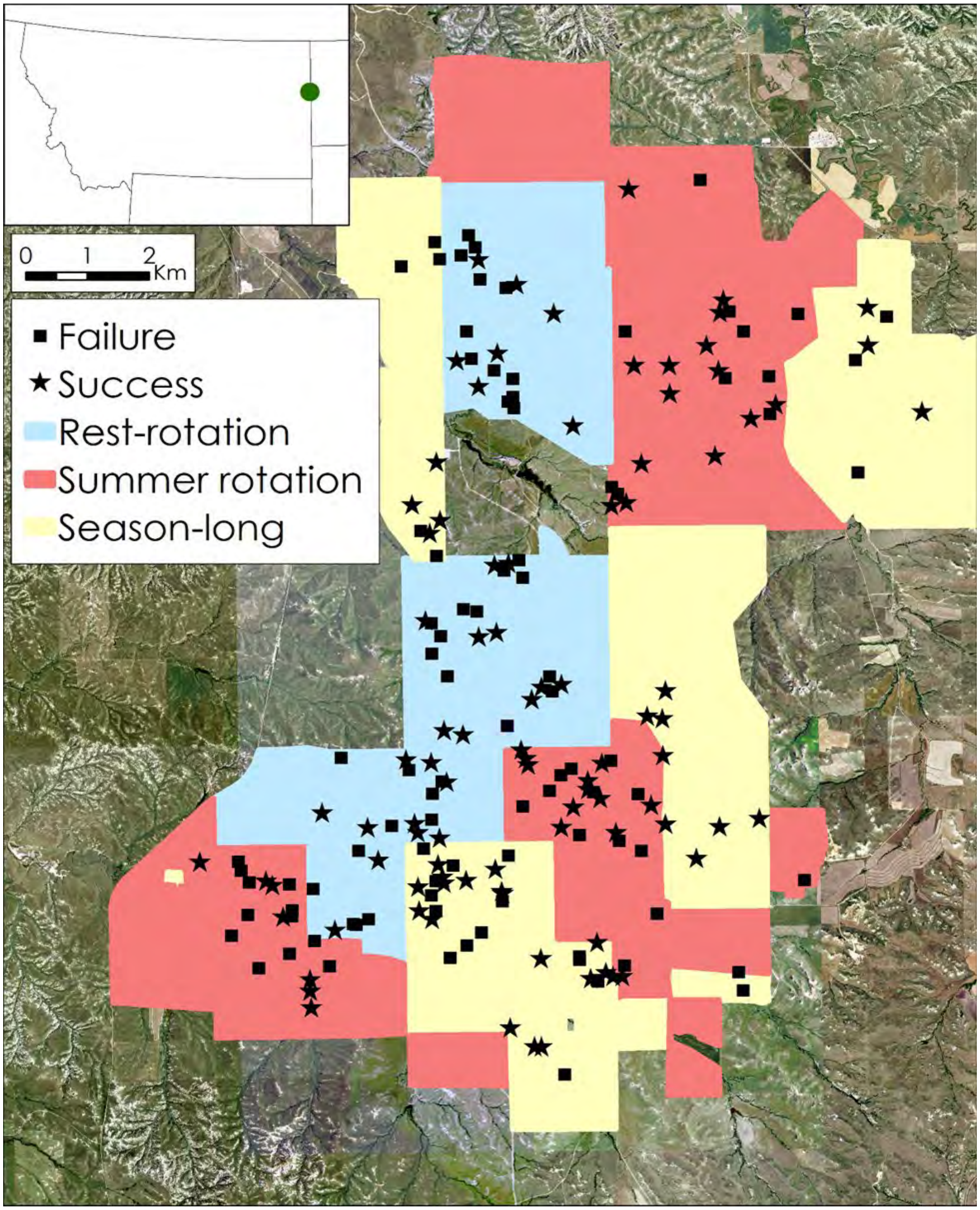

Figure 1. Locations of successful (stars) and failed (squares) sharp-tailed grouse nests in 2016–18 in relation to different grazing treatments.

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 (ΔAICc = 0.50 – 1.83, wi = 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 (ΔAICc = 0, wi = 0.35) and proportion grassland marginally improved model fit compared to the null model (ΔAICc = 1.36, wi = 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 (ΔAICc = 0, wi = 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).

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

Management Analysis					
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

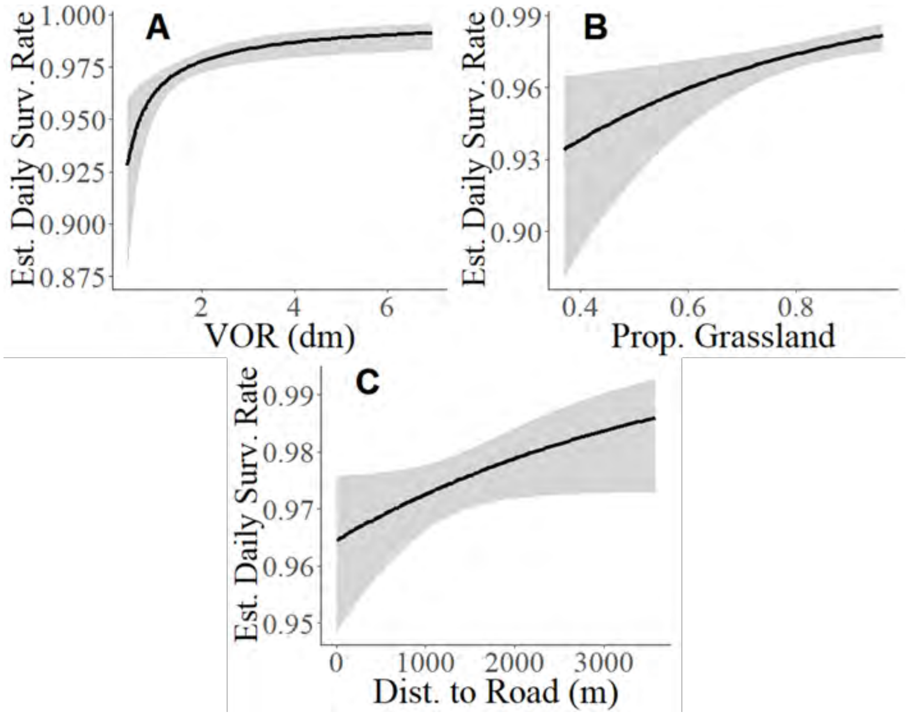

Figure 2. Estimated daily nest survival in relation to important habitat variables, with 85% confidence intervals shown in grey. Visual obstruction (VOR) was averaged across the 6 m vegetation plot.

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 (± 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 (ΔAICc = 0, wi = 0.90, Table 3), with confidence intervals for all three variables not overlapping zero, suggesting significant effects.

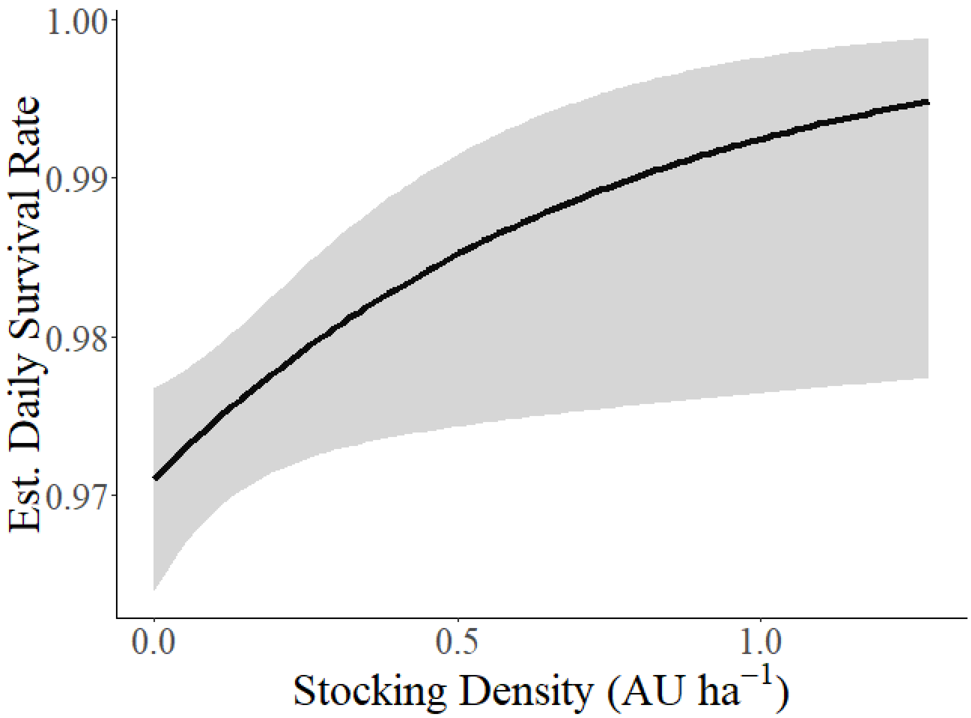

Figure 3. Estimated daily nest survival in relation to stocking density while the nest was active, with 85% confidence intervals shown in grey.

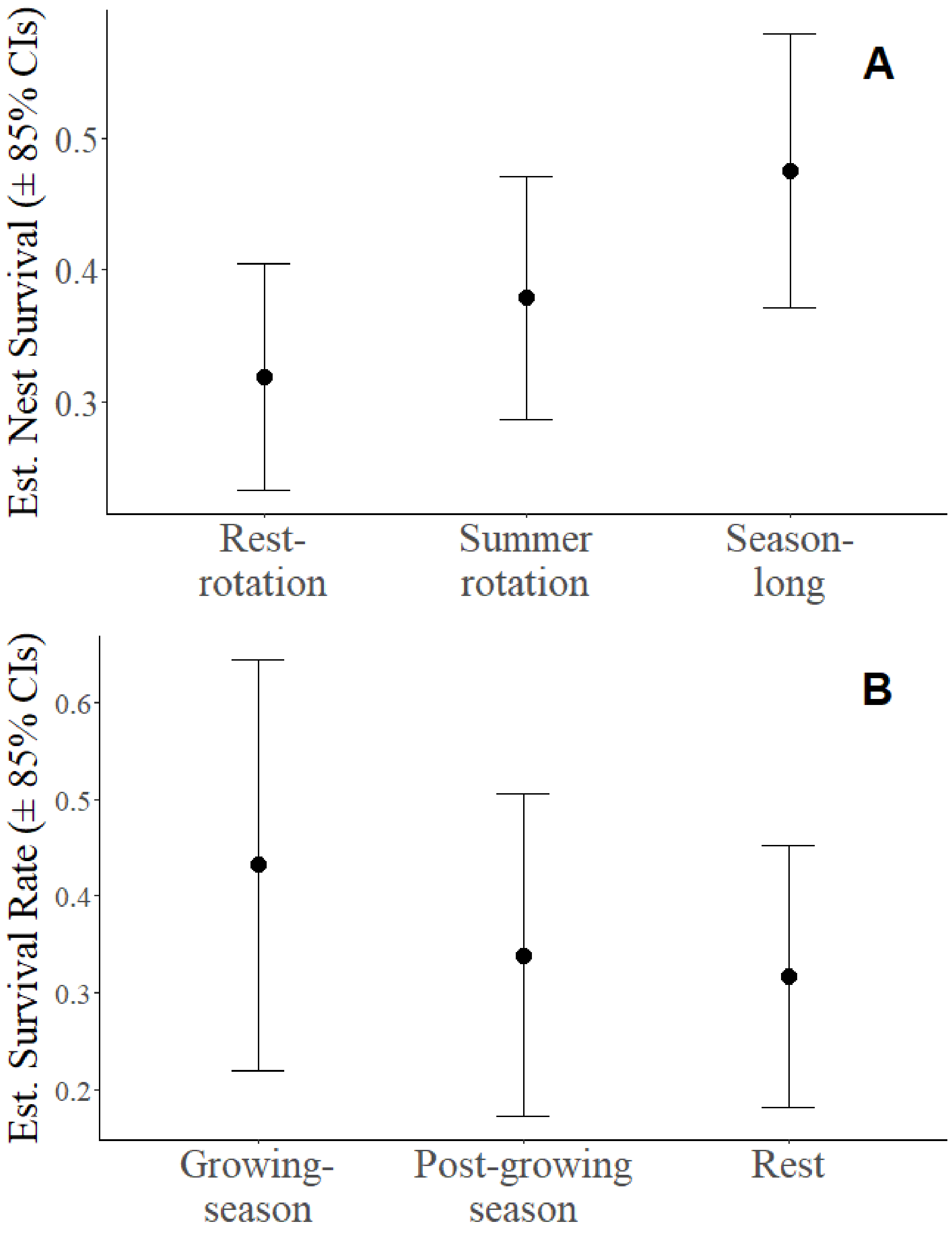

Figure 4. Estimated overall nest survival (± 85% confidence intervals) for sharp-tailed grouse in each of the three grazing treatments (A) and in each of the three treatments within the rest-rotation system in 2016–18 (B).

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).

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

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.

Table 5. Sharp-tailed grouse brood survival (± 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 ± 0.10	0.55 ± 0.08
Summer rotation	30	0.80 ± 0.07	0.54 ± 0.06
Season-long	29	0.66 ± 0.09	0.59± 0.07
Multiple systems	14	0.43 ± 0.13	0.32 ± 0.09
Total	95	0.65 ± 0.05	0.54 ± 0.4

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.

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

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

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 (± 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).

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**
Breeding season						
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
Non-breeding season						
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

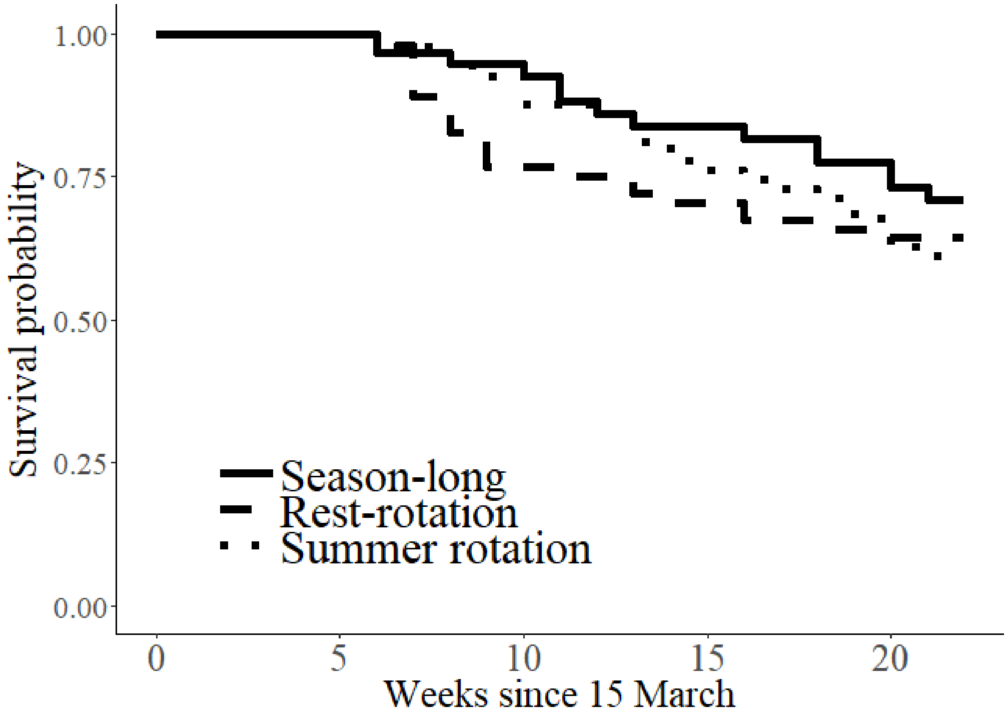

Figure 5. Kaplan-Meier plot of cumulative weekly survival during the breeding season of radio-marked female sharp-tailed grouse associated with 3 grazing systems in eastern Montana and western North Dakota. Confidence intervals omitted for clarity.

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).

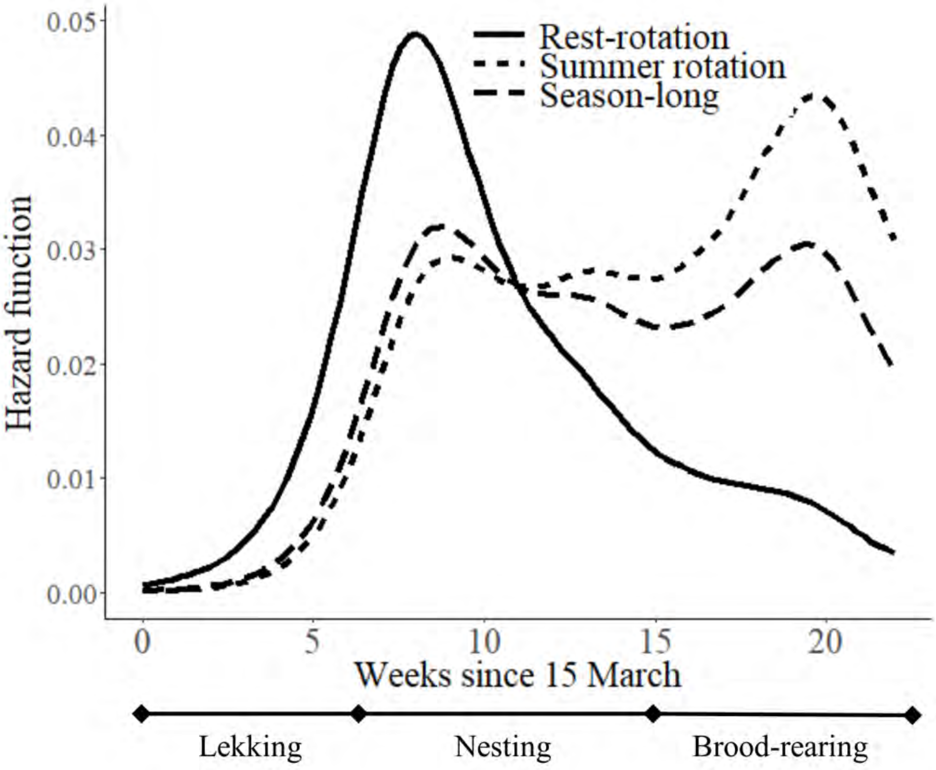

Figure 6. Weekly hazard functions during the breeding season for female sharp-tailed grouse associated with 3 grazing systems in eastern Montana and western North Dakota. Confidence intervals omitted for clarity. The approximate timing of lekking, nesting and brood-rearing activity is shown at the bottom.

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 (β = 0.02 ± 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).

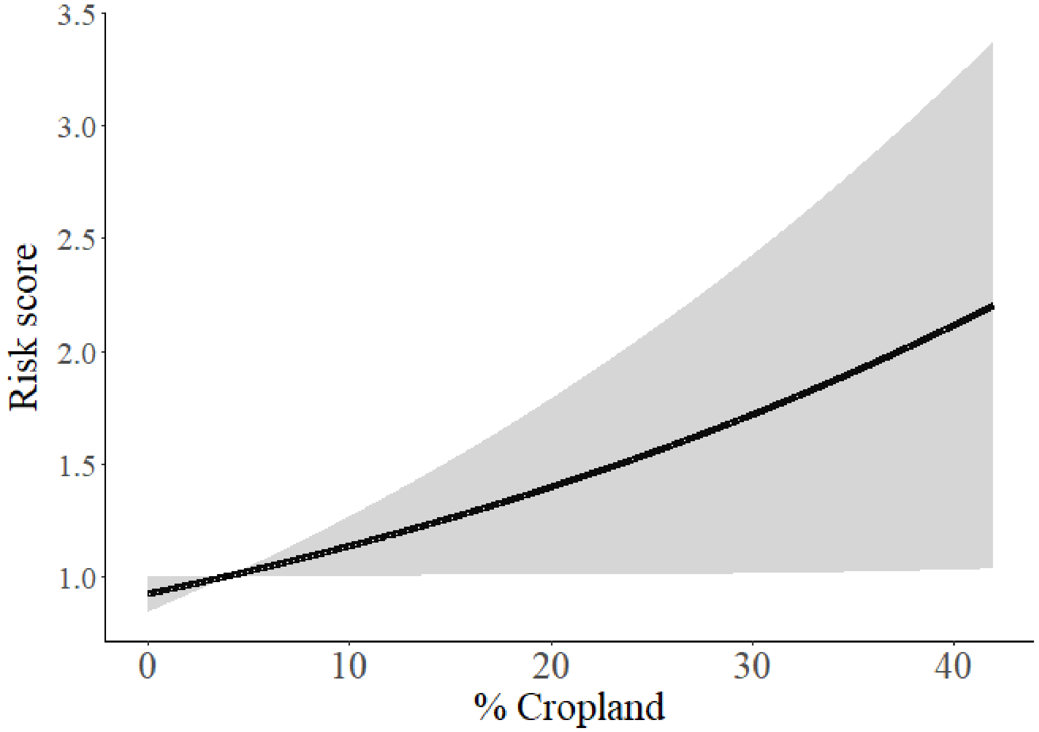

Figure 7. Risk score (± 85% confidence intervals) from an Andersen-Gill formulation of the Cox proportional hazards model estimating the risk of mortality for female sharp-tailed grouse relative to the percent agriculture within 1,300 m in eastern Montana and western North Dakota.

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 Monta.na 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

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:

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

$$Log(\lambda_y) = \alpha_0$$

Observation Process:

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

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

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 Lefkovitch 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:

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

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

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*(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:

$$F_{ja} = ((np1_a * cl1_{ja} * ns1_a * h_a * cs_{ja} * js_a) +$$

$$((1\text{-}ns1_{ja}) * np2_{ja} * cl2_{ja} * ns2_{ja} * h_a * cs_{ja} * js_a))/2.$$

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:

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

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

$$\gamma_j \sim Normal(0, \sigma\gamma^2)$$

where $y_{np2,j}$ represents the number of renests, $n_{np2,j}$ is the number of unsuccessful first nests in each year (*j*) and 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 $\sigma\gamma^2$.

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 $\beta_{\text{age},}$ nesting female stage class. Clutch sizes of firsts nests and second nests were modeled as being drawn from a Poisson distribution and estimated as:

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

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

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

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:

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

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

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

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:

$$\mu_{1yi} = \mathrm{N}_{s(1,y-1,i)} * \mathrm{R}_{(1,y-1)} * \mathrm{S}_{8(1,y-1)} +$$
$$\mathrm{N}_{s(2,y-1,i)} * \mathrm{R}_{(2,y-1)} * \mathrm{S}_{8(2,y-1)},$$

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:

$$\mathrm{N}_{1yi} \sim Poisson(\mu_{1yi})$$

We represent the number of yearlings surviving into adulthood ($\mathrm{N}_{\mathrm{new}(2yi)}$) 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.

$$\mathrm{N}_{\mathrm{new}(2yi)} \sim Binomial(\mathrm{S}_{12(1,y-1)}, \mathrm{N}_{(1,y-1,i)})$$

Similarly, the number of surviving adults from the prior year ($\mathrm{N}_{\mathrm{old}(2yi)}$) 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:

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

Given the information in the constructed Lefkovitch 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 ($N_{new(2yi)}$) and returning adults ($N_{old(2yi)}$) and total abundance (N_{tot}) is the sum of total adults (N_{2yi}) and yearlings (N_{1yi}):

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

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

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:

During the study period, we located 188 grouse nests laid by 128 individual females, of which 147 were first nests and 41 renesting attempts. Individual female hen, year, and female stage class did not significantly impact nest survival. We evaluated chick survival for 93 broods (2016; n = 25, 2017; n = 36, 2018; n = 32). To estimate adult survival, our data set consisted of information for 153 female sharp-tailed grouse, some of which were monitored in multiple years resulting in 172 bird years (2016; n = 55, 2017; n = 64, 2018; n = 61). Of the total bird years, 66 were females primarily using rest-rotation, 46 primarily used season-long, and 60 used summer rotation.

Estimated vital rates (Tables 9-11) 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.

Table 9. Estimates and 95% credible intervals for fecundity parameters in 2016 from a female-based integrated population model on Sharp-tailed grouse in western Montana.

	Yearling		Adult	
Parameter	Estimate	95% CrI	Estimate	95% CrI
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 10. Estimates and 95% credible intervals for fecundity parameters in 2017 from a female-based integrated population model on Sharp-tailed grouse in western Montana.

	Yearling		Adult	
Parameter	Estimate	95% CrI	Estimate	95% CrI
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 11. Estimates and 95% credible intervals for fecundity parameters in 2018 from a female-based integrated population model on Sharp-tailed grouse in western Montana.

	Yearling		Adult	
Parameter	Estimate	95% CrI	Estimate	95% CrI
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)

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 12). 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 13); 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.

Table 12. 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.

	grazing system			
	rest-rotation		**summer rotation**	
parameter	**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 13. Posterior mean estimates and 95% credible intervals of finite rate of population change (λ), 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 *during* 2016– 2018.

			95% CrI		
Parameter	Year	Estimate	LL	UL	Rhat
juvenile survival		0.402	0.343	0.464	1.000
λ	2016 to 2017	0.741	0.615	0.874	1.001
λ	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

Products Resulting from Objective 1

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., and L.B. McNew. 2019. Effects of scavenging on assumptions of mortality analyses of radio-marked gamebirds. Northwestern Naturalist 100:197–205.

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.

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. and L.B. McNew. In press. Does researcher activity impact the nest survival of sharp-tailed grouse? Wildlife Biology, accepted 5/2021.

M.C. Milligan, Lipinski, A.R., and L.B. McNew. In review. Evaluating the cumulative effects of livestock grazing on wildlife with an integrated population model. Paper abstract accepted for special issue of Frontiers in Ecology and Evolution.

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

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 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 ≥ 60% of the home range. Females were considered to use multiple systems if no one system accounted for ≥ 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 critierion (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 14). 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 15). Density of edge habitat within the home range was the best predictor of home range size (Table 15) and was negatively related to the size of breeding season home ranges ($\beta = -5.26 \pm 1.48$; Fig. 9).

Table 14. 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 ≥ 60% of their home range or were considered to use multiple systems if no one system accounted for ≥ 60% of their home range.

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

Table 15. 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, AIC$_c$ values, model weights (*w$_i$*), and log-likelihoods are reported.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**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 16. 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

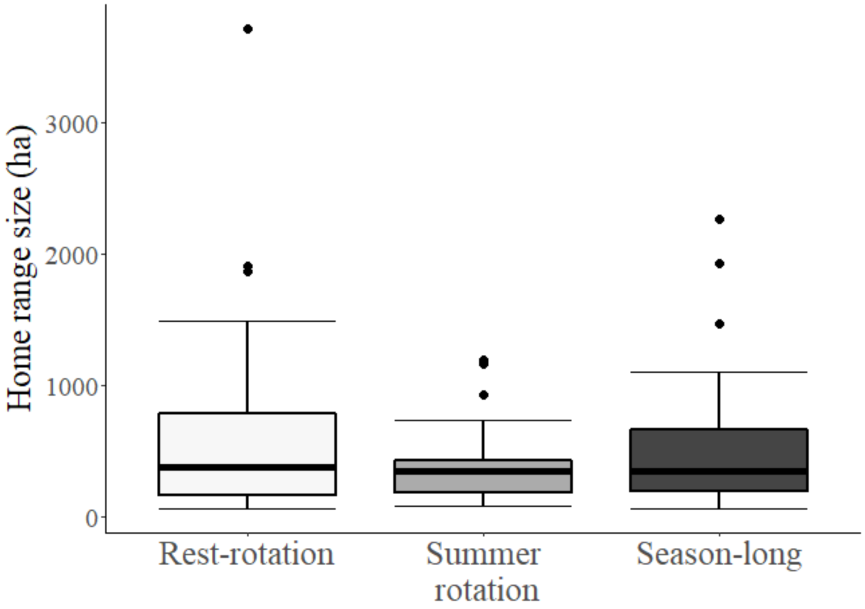

Figure 8. Female sharp-tailed grouse breeding season home range size (± SE) by grazing system. An individual female was assigned to a grazing system according to the system containing ≥ 60% of the individual's home range.

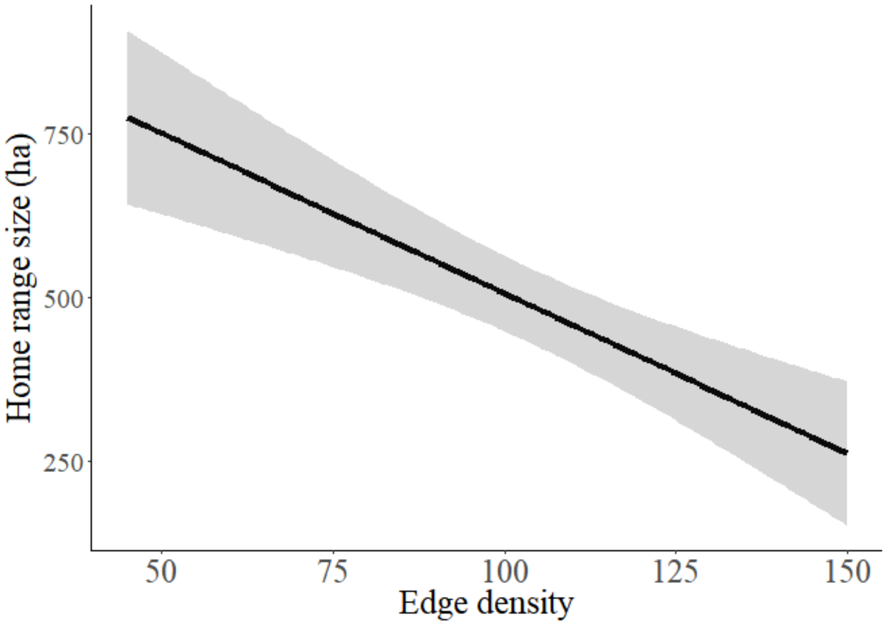

Figure 9. Relationship (± 85% confidence intervals) between the density of edge habitat (total landcover edge length / polygon area) and breeding season home range size for female sharp-tailed grouse.

At the second order, breeding season habitat use was ranked as follows: grassland = wooded draws >> other (primarily ruderal grasslands) >> cropland (Table 16), 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.

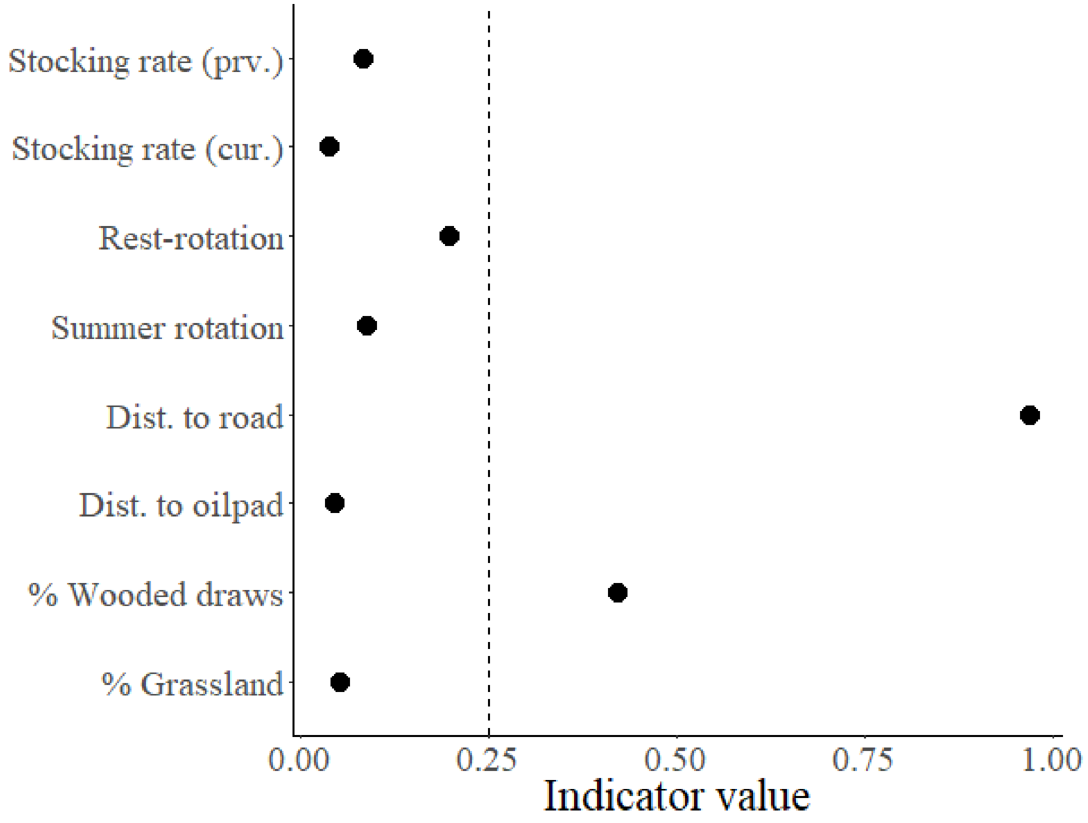

Figure 10. Bayesian variable selection identifying important predictors of sharp-tailed grouse third-order habitat selection during the breeding season. Predictors with indicator variables ≤ 0.25 are considered unimportant.

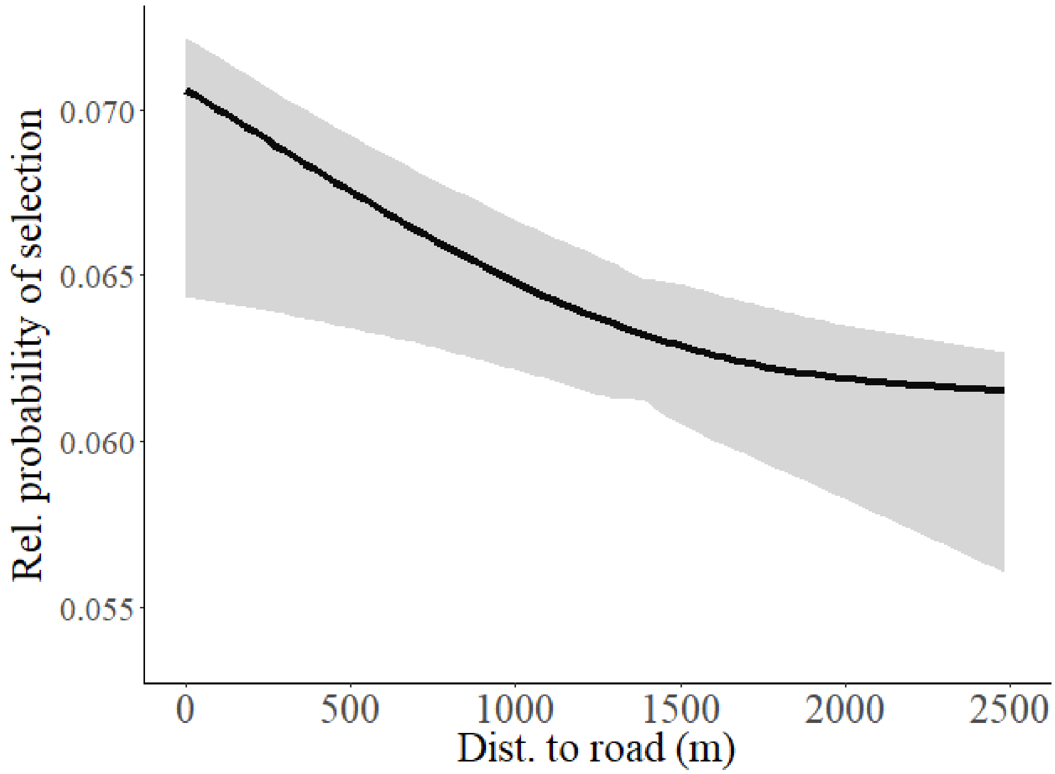

Figure 11. Relationship (± 95% credible intervals) between the distance to a road and the relative probability of selection of female sharp-tailed grouse within the breeding season home range.

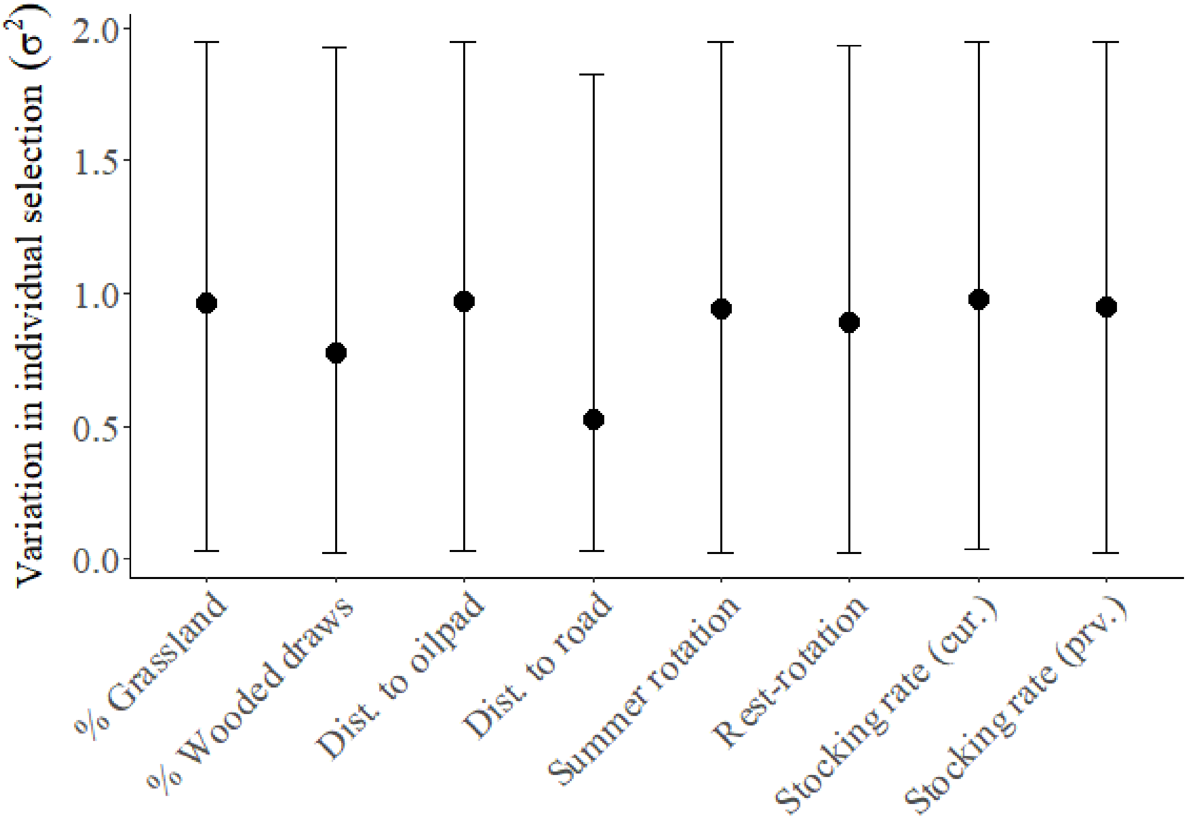

Figure 12. Posterior estimates of the variability in selection (σ2 ± 95% credible intervals) among individual female sharp-tailed grouse for each habitat variable. σ2 is a measure of how strongly individuals varied in selection for different habitat variables. Habitat variables were scaled prior to model fitting.

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 (ΔAICc = 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 (ΔAICc = 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 (ΔAICc = 0, $w_i = 0.61$, Table 17). 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 (β = 0.48 ± 0.17) and shrubs (β = 0.33 ± 0.20) had small but positive effects on the relative probability of selection, while selection decreased with increasing fragmentation or MSI (β = -0.50 ± 0.16). Visual obstruction at the nest bowl had the largest effect on the relative probability of selection (β = 11.45 ± 1.31), with selection increasing up to a threshold of 20–30 cm (Fig. 13).

Table 17. 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
Management Analysis						
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

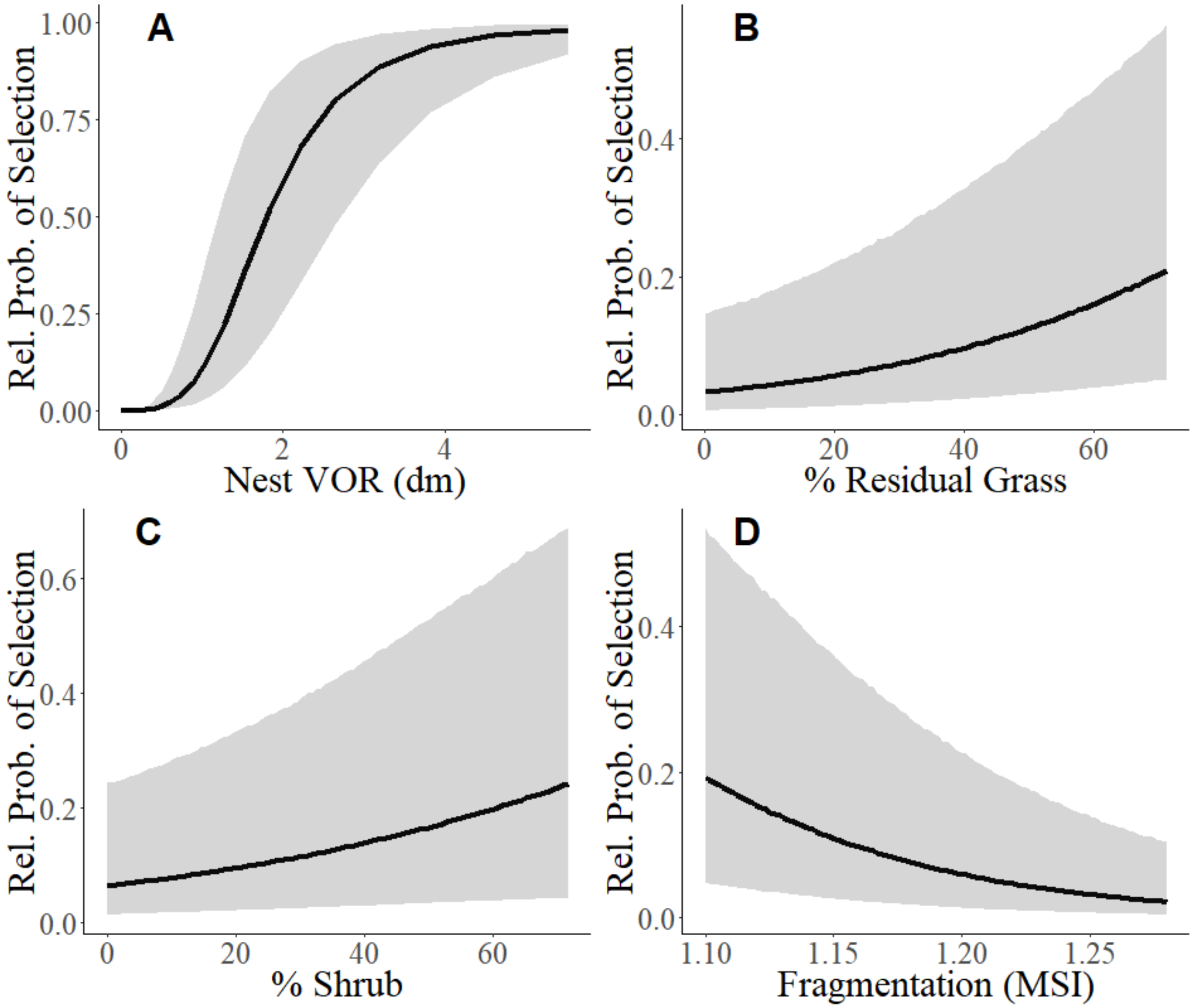

Figure 13. Estimated relative probability of nest site selection in relation to important habitat variables, with 85% confidence intervals shown in grey. Visual obstruction (VOR) was measured at the nest bowl.

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 (β = -0.17 ± 0.10). However, in the full analysis, the model containing habitat variables (ΔAICc = 0, w_i = 0.58) outperformed models with management-level variables (Table 17), 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 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).

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 captured grouse at 12 leks during the months of March–May using walk-in funnel traps. Females were fitted with VHF radio transmitters (model A4050; Advanced Telemetry Systems, Isanti, MN). Females with broods, determined by systematic brood flushes, were located remotely by triangulation at least 3 times/week during the breeding season (March–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. All animal handling was approved under Montana State University’s Institutional Animal Care and Use Committee (Protocol #2016-01).

We obtained a map of soil map units, ecological sites and their accompanying ecological site descriptions (ESDs) collected by rangeland conservationists and soil scientists at the USDA-NRCS office in Richland County, Montana. 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) and Doherty et al. (2011).

During 18 June – 4 July, 2018, we measured the condition within each ecological site at the study area using a similarity index to compare the current plant community to the historic plant community obtained from the ESDs (United States Department of Agriculture 2006). Each day, we calibrated our ocular estimates of similarity index at 10 randomly selected locations where we visually estimated the percent decreaser graminoid species contained in a 1 × 1-m plot. We then clipped vegetation in the plot and divided into two bags; one bag contained only decreaser grass species and the other contained all other vegetation (increaser grasses, forbs, shrubs, etc.). Both bags were weighed to estimate percentage dry weight of plant material at the current growth stage. We calculated the similarity index by dividing the weight of the decreaser graminoids to all other clipped vegetation to calibrate our visual estimates of proportion decreaser graminoids at within each ESD. After calibration, we conducted pasture-level surveys by walking pastures and estimating similarity index for each ESD polygon at a scale of 1 ha or greater (United States Department of Agriculture 2006). The similarity index was divided thematically into 5 classes: very low, low, moderate, high, and very high (Table 1). We then mapped the similarity index to each ESD polygon using ArcMap 10.6.1 (Environmental Systems Research Institute, Redlands, CA).

We evaluated whether soil type, ESD, and similarity index were related to vegetation conditions previously found to influence habitat selection by sharp-tailed grouse (Milligan et al. 2018) at a subset of brood and paired locations within a study area defined by a minimum convex polygon around the leks of capture and buffered to 2 km (Connelly et al., 1998). Points that were inaccessible (e.g., in water, cultivated fields, on properties we did not have permission to access) were replaced. At these sites, we recorded visual obstruction readings (VOR; Robel et al., 1970) at the point and four points located 6 m from the center point. VOR was measured at each point in all four cardinal directions from a distance of 2 m and a height of 0.5 m (Milligan et al., 2020). 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 a 20 × 50 sampling frame (Daubenmire, 1959). Vegetation surveys at brood locations and paired random locations occurred within 3 days of identified use.*Statistical Analyses*

2nd Order Selection. – We examined second order selection, or selection of brood home ranges within the study area, using resource selection functions where use was evaluated for individuals and available habitat evaluated for the study population (design 2; Thomas and Taylor 1990). Available habitat was defined collectively for the population by as the 95% utilization distribution calculated for all locations across all three years within the study area using the adehabitat package in Program R (Aebischer et al. 1993). We plotted random points inside this study area polygon at a 1:40 ratio of used:available points (Milligan et al., 2020b). We transformed similarity index from a discrete ordinal variable with 5 classes to a continuous variable by using the midpoint value of similarity for each class. We developed spatially stationary RSFs where brood locations (use) and random points (available) were considered independent samples (Manly et al. 2002). We initially fitted generalized linear mixed models (GLMMs) with the logistic link function and a binomial error structure to evaluate RSFs, where brood identity was included as a random intercept in all models. However, initial model fits did not support inclusion of the random intercept term based upon evaluations of conditional and marginal R2, indicating a lack of autocorrelation of selection within individual broods (Nakagawa and Schielzeth 2013; Wyffels et al. 2020); we therefore fitted our RSFs with fixed effects only generalized linear models. Candidate models included main effects of soil type, ecological site description, and similarity index. We evaluated all univariate and additive combinations as well as an interaction model to test the hypothesis that the effect of ESD on habitat selection is mediated by similarity index. Models were then compared using Akaike's Information Criterion (AICc); models with ΔAICc values ≤ 2 were considered parsimonious (Anderson and Burnham 2002). Effects were considered significant predictors of selection if estimated 95% confidence intervals did not include 0 (Arnold 2010). All statistical analyses were performed in R statistical software (ver. 4.0.2; R Development Core Team 2020, Vienna, Austria), where GLMMs were fit with the lme4 package (Bates et al. 2012).

3rd Order Selection. – We examined the effects of ESD and similarity index on brood site selection using RSFs as described for 2nd order selection, except habitat availability was specific to each brood (Manly et al., 2002). Locations of radio-marked brood hens were considered used and random points were considered available following design 3 of Thomas and Taylor (1990) where a home range is defined for each individual and available points were sampled within the home range. Due to small and uneven sample sizes of used points among broods, home ranges were calculated using non-parametric minimum convex polygons with the adehabitat package in Program R. Minimum convex polygons of broods that had ≤ 5 locations were buffered by 200 m, the average distance moved by female grouse during the breeding season in our study, to prevent under-sampling areas that were available to each brood. Random points were plotted inside the home range of each brood at a 1:40 ratio of used:available points. Ecological site type (ESD) and similarity index were assigned to each used and available point using our spatial map. We evaluated competing models with fixed effects of ecological site description, similarity index, their additive and interaction effects, and soil type using AICc. We included a null model in the candidate set and evaluated support for predictor effects based on evidence ratios and 95% confidence intervals of estimated effects (Anderson and Burnham 2002; Arnold 2010).

We could not evaluate the effects of fine-scale vegetation conditions on brood habitat selection because we did not measure vegetation conditions at every brood location and random available point. Instead, we calculated descriptive statistics (e.g., means, standard deviation) for fine-scale vegetation (e.g., habitat) conditions at a subset of randomly sampled locations in relation to soil type, ESD, and similar index.

Results

We documented 845 brood use locations from 72 individual broods during May–August, 2016–2018. Three ESDs comprised approximately 88% of the study area (Table 18). Brood use locations were distributed broadly across ESDs; brood locations occurred in 10 of the 12 ESDs identified within the study area. Although the majority (69%) of brood locations occurred in ecological sites described as silty, selection ratios indicated potential preferences for a variety of ESDs (Table 18). Brood locations occurred in 15 of 21 soil types available within the study area (Fig. 14); however, 81% of brood locations occurred in four soil types (Table 18). The average ± SD similarity index across the study area was 37 ± 16% with 98% of the study area having similarity index of ≤ 60% (very low – moderate similarity). The average similarity index at brood use locations was 35% ± 16%.

Table 18. Number and proportions of brood use locations relative to availability on the study area in Richland County, Montana, 2016–2018.

	# Brood Locations	Proportion of Brood Locations	Proportion Available	Selection Ratio
Ecological Site				
Clayey	1	0.0012	0.0005	2.40
Gravelly	15	0.0178	0.0155	1.15
Shallow Loamy	158	0.187	0.0055	34.00
Loamy – Rolling Soft Shale	35	0.0414	0.1134	0.37
Limy Residual	36	0.0426	0.036	1.18
Silty-Sedimentary	288	0.3408	0.0363	9.39
Silty-Steep	295	0.3491	0.4635	0.75
Saline Upland	12	0.0142	0.3079	0.05
Saline Lowland	5	0.0059	0.0013	4.54
Soil Type[a]				
201C	101	0.1195	0.1102	1.08

202D	137	0.1621	0.2437	0.67
53C	36	0.0426	0.0363	1.17
53D	158	0.187	0.1134	1.65
BmB	12	0.0142	0.0069	2.07
CeA	14	0.0166	0.0362	0.46
CeB	5	0.0059	0.0115	0.51
E2147C	35	0.0414	0.0360	1.15
Lc	6	0.0071	0.0327	0.22
LfF	289	0.342	0.2596	1.32
Lo	1	0.0012	0.0005	2.28
ShA	4	0.0047	0.0243	0.19
ShB	27	0.032	0.0369	0.87
TeF	15	0.0178	0.0155	1.15
Tw	5	0.0059	0.0062	0.96
CeC	0	0		

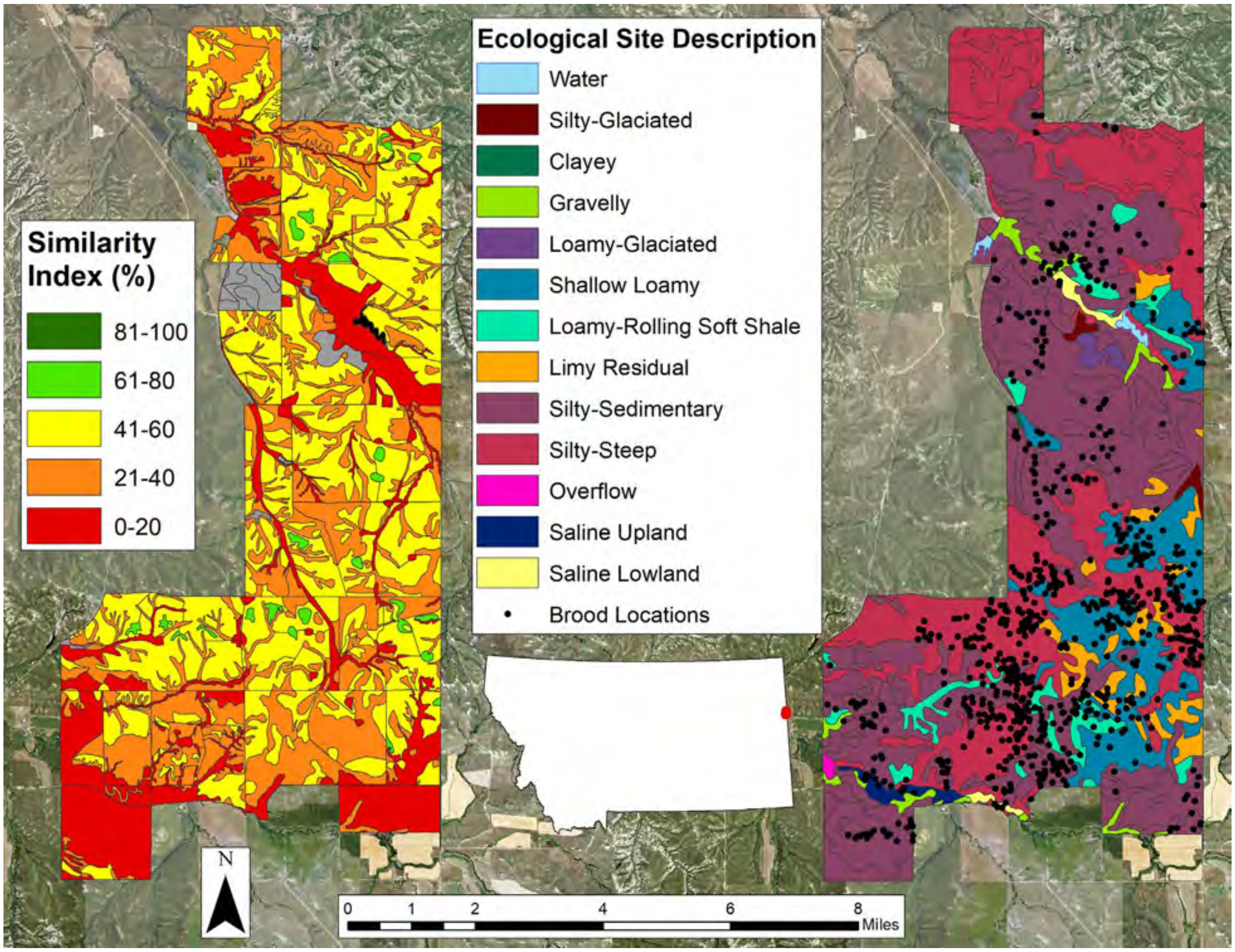

Figure 14. Similarity index and ecology sites within the study area in eastern Montana.

Habitat selection by broods

The effect of soil type on second-order selection of home ranges by brood hens had high relative support ($\Delta \mathrm{AIC_c} = 0$, wi > 0.99). Models that included the effects of ESD and similarity index, as well as a null model, received virtually no support (Table 19). Selection of some soil types (e.g., 53D) by broods was high relative to others (e.g., ShA), and we did not document brood use in six soil types (Table 19; Fig. 15). We also observed relatively high selection ratios for BmB and Lo soil types. However, these soil types were rare (<1% of the study area) and the number of brood use locations were few; 13 of 845 brood locations (1.5%) occurred at BmB and Lo sites. Productivity index scores were similar between soil types with selection ratios >1 (42 ± 35SD) and those with ratios <1 (51 ± 35).

Within home ranges, third-order habitat selection by broods was best predicted by similarity index. A model that included just similarity index had most of the support ($\mathrm{AIC_c}\ w_i = 0.81$) and models that included similarity index had virtually all support (cumulative $\mathrm{AIC_c}\ w_i > 0.99$; Table 19). The relative probability of selection decreased as similarity index increased ($\beta = -0.78 \pm$

0.22; Fig. 16). We found little evidence that ecological site type had an effect on relative brood habitat selection within home ranges ($\Delta\text{AIC}_c = 10.5$, wi < 0.001), and our hypothesis that ESD interacted with similarity index to influence habitat selection was also not supported (ΔAIC_c $w_i < 0.001$; Table 19).

Table 19. Support for candidate models predicting second- and third-order selection of brood-rearing female sharp-tailed grouse during 2016–2018.

Model	K	AIC$_c$	ΔAIC$_c$	AIC$_c$ w_i	Cumulative w_i
2nd Order Habitat Selection					
Soil Type	21	7797.63	0.00	>0.99	1.00
Ecological Site × Similarity Index	21	7835.72	38.09	<0.01	1.00
Ecological Site + Similarity Index	13	7853.01	55.39	0.00	1.00
Ecological Site	12	7854.32	56.69	0.00	1.00
Null (constant model)	1	7914.65	117.02	0.00	1.00
Similarity Index	2	7916.63	119.00	0.00	1.00
3rd Order Habitat Selection					
Similarity Index	2	7863.03	0.00	0.81	0.81
Ecological Site × Similarity Index	19	7867.01	3.98	0.11	0.92
Ecological Site + Similarity Index	11	7868.10	5.06	0.06	0.98
Soil Type	18	7872.77	9.74	0.01	0.99
Null (constant model)	1	7873.21	10.18	<0.01	1.00
Ecological Site	10	7873.52	10.50	0.00	1.00

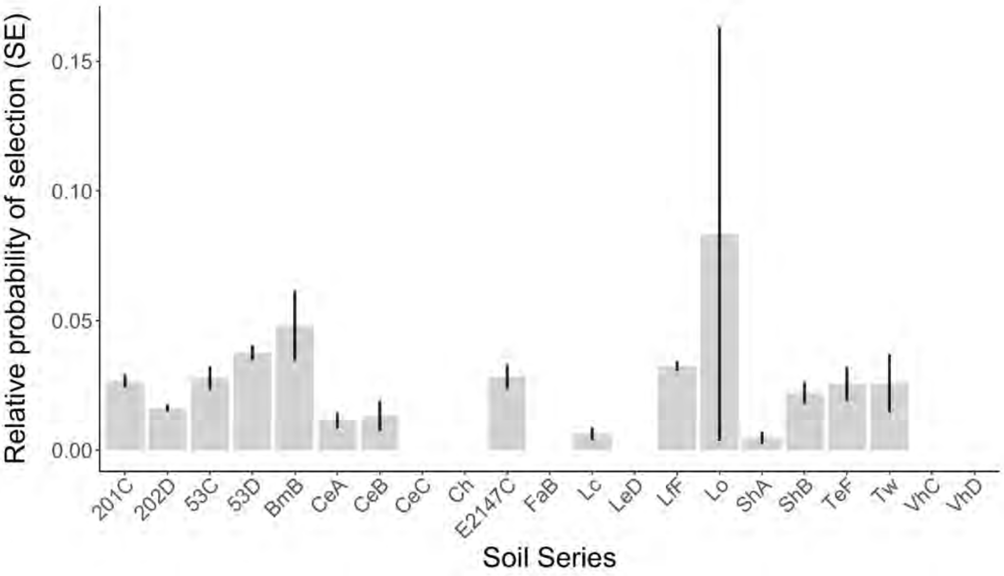

Figure 15. Relative probability of second-order selection by sharp-tailed grouse broods relative to soil type in eastern Montana, 2016–2018.

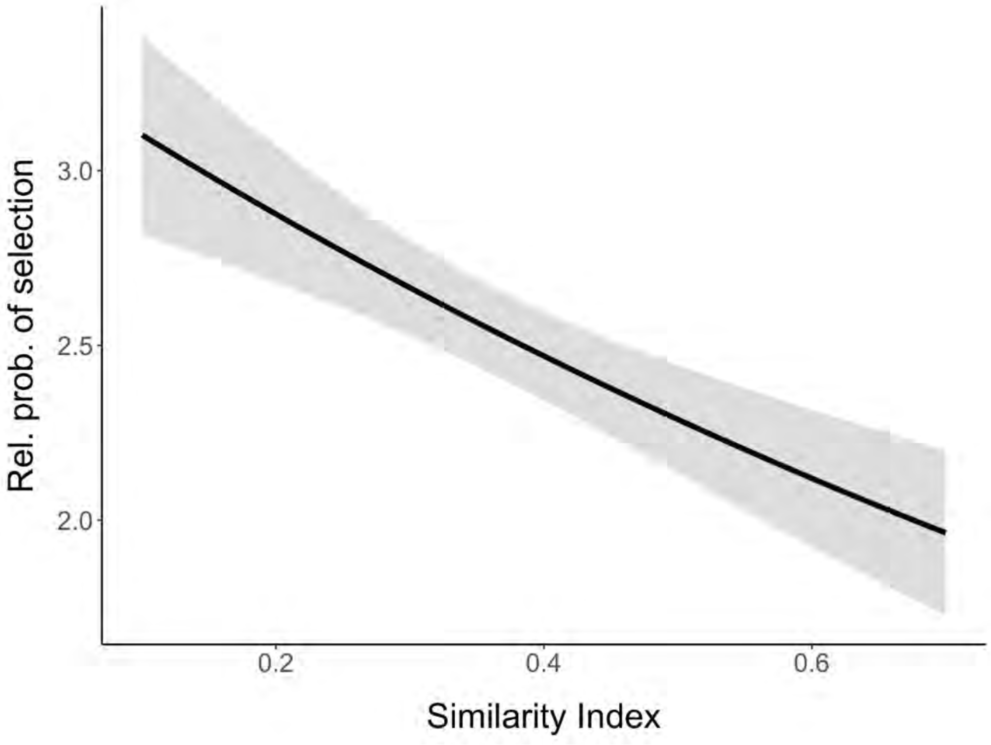

Figure 16. Predicted effect of similarity index on the relative probability of third-order brood selection in eastern Montana, 2016–2018.

Habitat Conditions

Vegetation conditions were variable across and within soil map units (Fig. 4). With the exception of shrub cover, average vegetation conditions were similar across categories of similarity index (Fig. 4). However, variability in VOR tended to decline with similarity index (Table 1). Average VOR was 1.78 ± 1.41SD, 1.09 ± 0.74, and 2.45 ± 0.55 dm in areas classified as very low, moderate, and high similarity index, respectively. Nevertheless, areas classified as having high similarity were rare (n = 2 sampling points) and no sites were classified as having very high similarity (Table 1). Forb cover was also somewhat higher and much more variable within sites with very low similarity index relative to sites with moderate and high similarity index (Table 20; Fig. 17). Higher similarity indexes were associated with higher shrub coverages; average ± SD shrub coverages were 2.8 ± 4.9% and 16.5 ± 13.3% for the very low and very high similarity index classes, respectively (Fig. 17).

Table 20. Similarity index classes, values, coverage of the study area, and associated vegetation conditions (VOR[a] and % forbs) considered important to sharp-tailed grouse broods in eastern Montana, 2016-2018.

Similarity Index (%)	Class	% Decreaser Graminoids	% of Sampling Points	VOR[a] mean ± SD	CV VOR	% Forbs mean ± SD	CV % Forbs
81-100	Very high (VH)	>50	0	--	--	--	--
61-80	High (H)	40	3	2.46 ± 0.54	0.22	6.6 ± 0.14	0.02
41-60	Moderate (M)	30	46	1.09 ± 0.73	0.67	8.3 ± 4.81	0.58
21-40	Low (L)	20	34	1.67 ± 1.08	0.65	8.2 ± 4.56	0.55
0-20	Very low (VL)	<10	17	1.78 ± 1.41	0.79	14.1 ± 12.0	0.85

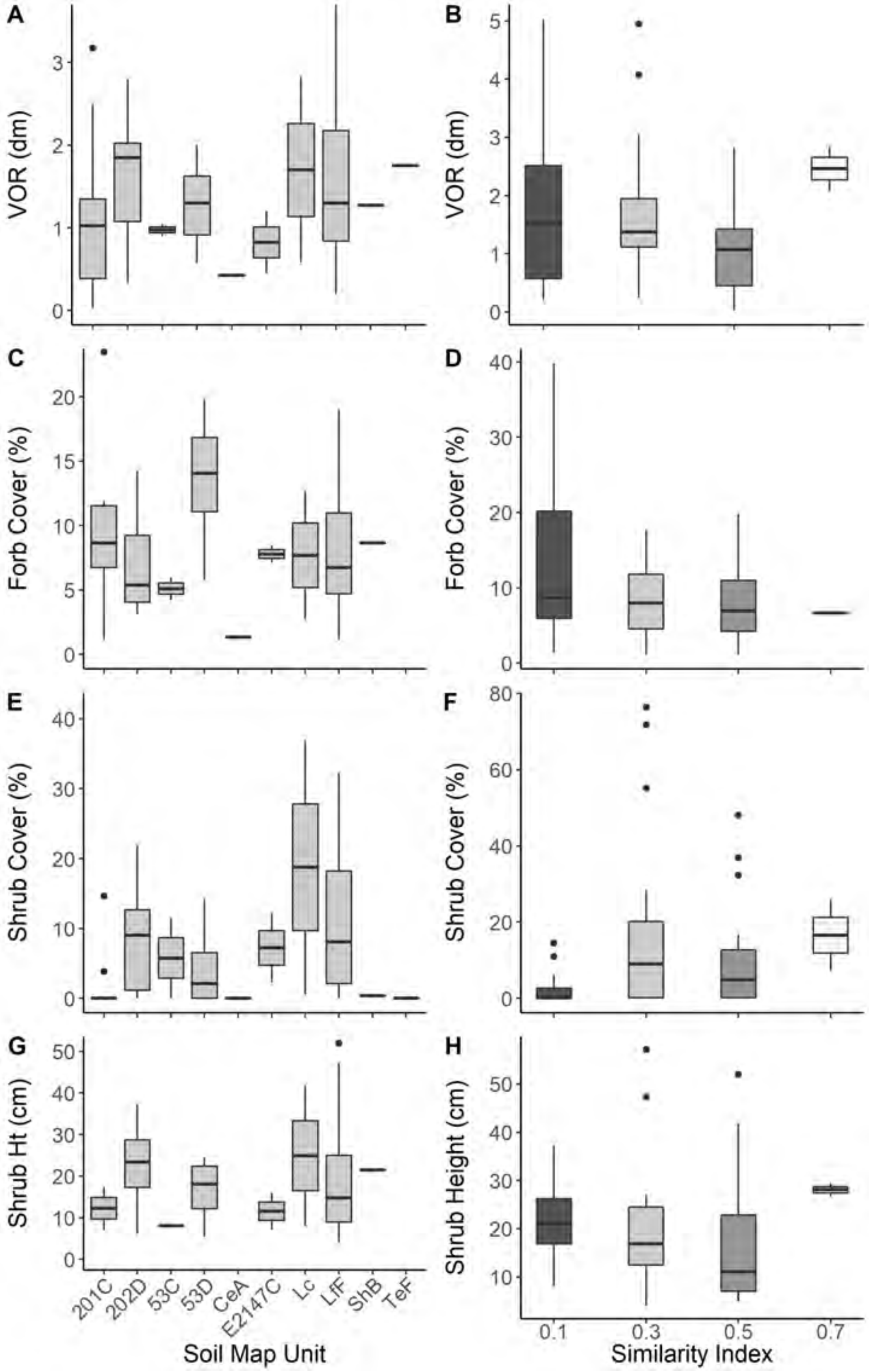

Figure 17. Boxplots of fine-scale vegetation conditions relative to soil map unit (soil type) and similarity index in eastern Montana, 2016–2018. Vegetation was measured at random points.

Products Resulting from Objective 2

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.

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.

Macon, L.K., M.C. Milligan, J.C. Mosley, and L.B. McNew. In review. Habitat selection by sharp-tailed grouse broods in relation to common rangeland management indicators. Submitted to Rangeland Ecology and Management.

Objective 3: Evaluate 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 meso-predator communities

Objective 3a: Effects of livestock grazing management on grassland birds abundance and community structure

Methods:

We surveyed grassland birds and vegetation at 610 points (305 each season) randomly located across gradients of habitat conditions within the Montana FWP UGBEP, managed under rest-rotation grazing (300 points; Hormay, 1970), and on adjacent lands managed under season-long (120 points) or 2-pasture summer-rotation (190 points) grazing systems. Of the three grazing systems evaluated, we had 3 replications of each rest-rotation and summer-rotation systems and 2 replications of season-long grazing systems. Within the 3-pasture rest-rotation grazing systems, cattle were turned out to the first pasture in late May, moved to the second pasture mid-August, and were removed for the season after 8 – 10 weeks; the third pasture in the system was rested from grazing. Season-long grazing systems in the study area allowed cattle to graze continuously from May or early June through October or mid-November. Within 2-pasture summer-rotation grazing systems in the study area, cattle were turned out to the first pasture in early June, moved to the second pasture after 6 – 8 weeks, and were removed early-mid November. At the scale of each management unit, rest-rotation grazing systems had a mean annual stocking rate of 2.82 AUM $\cdot$ ha^{-1} (range 2.29 – 3.34 AUM $\cdot$ ha^{-1}), summer-rotation systems had a mean stocking rate of 1.98 AUM $\cdot$ ha^{-1} (range 1.61 – 2.66 AUM $\cdot$ ha^{-1}), and season-long systems had a mean stocking rate of 1.24 AUM $\cdot$ ha^{-1} (range 0.8 - 1.5 AUM $\cdot$ ha^{-1}; Table S2).

Point-Count Surveys. – We collected data during two grassland bird breeding seasons (May – June, 2016–17). Avian point-count surveys began after all grassland bird species had arrived for the breeding season and were completed within a 4-week period to assume breeding population closure. To avoid double counting of individuals and assure statistical independence, survey points were spaced > 300 m apart. Points were located > 200 m from pasture boundaries to avoid counting birds using multiple pastures, and were located > 400 m from oil pads and > 250 m from gravel roads to control for bird avoidance of these areas (Thompson et al., 2015). We conducted three consecutive, yet independent 5-minute point-count surveys at each point. This survey method maximized observer efficiency, while simultaneously achieving population closure between survey visits, an assumption for statistical modeling of these types of count data

(Royle, 2004; Kéry et al., 2005). A single trained observer identified and tallied all birds detected visually or aurally within 100 m of the survey point (Ralph et al., 1993). At each survey location, the observer recorded the date, time, and wind speed. Point-count surveys were conducted from one-half hour before sunrise through no later than 0900h MST. We did not conduct bird surveys if average wind speed exceeded 16 km/hr, or during rainfall.

We defined grassland-associated species as those which have become reliant upon grassland habitat for part or the entirety of their life cycle (Vickery et al., 1999). We selected three focal species as representative of three broader guilds or assemblages of grassland bird species with overlapping niche requirements within their habitats (Root, 1967), the grasshopper sparrow (*Ammodramus savannarum*), vesper sparrow (*Pooecetes gramineus*), and western meadowlark (*Sturnella neglecta*). These three ground-nesting obligate grassland species have specific habitat requirements of native grasslands for breeding, recruitment, and survival throughout the summer grazing season (Poole, 2005). Habitat preferences for each of these three species are variable across ecoregion, but in the northern mixed-grass prairie, grasshopper sparrows generally select for moderate to high vegetation height, density, and litter availability (Dechant et al., 2003b; Fritcher et al., 2004; Lipsey and Naugle, 2017), thus representing the dense-grass guild at our study area. Vesper sparrows are often associated with lower vegetation densities and have a higher tolerance for shrub encroachment within grassland habitats (Browder et al., 2002; Dechant et al., 2003a), and represent the sparse-grass guild. Western meadowlarks are typically considered habitat generalists and are often one of the most common species within grassland habitats of the western United States (Davis and Lanyon, 2008), thus representing the generalist guild.

Vegetation Surveys. – We measured local vegetation conditions within bird survey areas the same day point-count surveys were conducted. We established three 20-m transects of 5 subplots per transect within 100 m of each survey point, with one transect located at the survey point and oriented in a random direction, and two transects located and oriented randomly within 100 m of the point. At each subplot, we measured visual obstruction from the north at a distance of 2 m and a height of 0.5 m (VOR; Robel et al., 1970) and vegetation coverages using methods of Daubenmire (1959), where overlapping coverages of residual grass, litter, forb, and bare ground were recorded in one of six percentage classes (0–5, 5–25, 25–50, 50–75, 75–95, and 95–100 %). Midpoints of percentage classes were recorded for each vegetation coverage measurement. We measured heights (cm) of the nearest plant to the center of the frame for each residual grass and litter. We also conducted line-intercept surveys along each transect to estimate shrub foliar cover (hereafter "shrub cover") within point-count survey areas. The species of each shrub intersecting the transect was recorded, as well as the height and length of the shrub as it crossed the transect (Canfield, 1941). We used ArcGIS 10.4 (ESRI, 2011) to digitize the wooded coulees and pasture fences within the study area using five band 1-m resolution aerial imagery from the National Agricultural Imagery Program (NAIP) available through the USDA Farm Service Agency. From these digitized layers, we derived the total area of wooded coulees and fences to calculate relative densities within and surrounding bird survey areas.

In uneven terrain, randomly generated survey points are often located on hillsides, which may reduce the ability of observers to see and hear birds. We used ArcGIS Spatial Analyst extension and a 10-m digital elevation model (DEM) raster layer to calculate viewshed size to model as a function of grassland bird detection probability (ESRI, 2011), defining viewshed as the area visible to the observer within 100 m of the bird survey point.

We quantified rangeland production potential associated with each bird survey area using Soil Survey Geographic Database (SSURGO) ecological site data from the Natural Resources Conservation Service (NRCS) Web Soil Survey (Lipsey and Naugle, 2017; USDA NRCS, 2017). We utilized these data as a reasonable index of average rangeland productivity (Relyea et al., 2000), as rangeland managers implement long-term livestock grazing systems based on the expected annual vegetation production of their rangelands in a normal year. We calculated the weighted average rangeland production potential within 100 m of each bird survey point, effectively accounting for point count survey areas which encompassed multiple ecological sites. We selected the production values under average precipitation, as weather conditions during our study were considered normal.

We obtained livestock numbers, weights, and turn-in/turn-out dates from our collaborating ranch managers and calculated stocking rates within our pastures based on an animal unit month (AUM), the amount of forage, measured on a dry weight basis, to feed a 1,000-lb animal for a 30-day period (Holechek et al., 2011). Pastures within our study area were stocked with a mixture of 1,300-lb cow-calf pairs and 800-lb yearling steers and heifers, which were considered 1.3 and 0.8 AU's, respectively. Stocking rates from the previous year's summer grazing season were used as a predictor of grassland bird abundance, as breeding territories had already been established within pastures prior to cattle turn-out dates in our study area (Ahlering and Merkord, 2016). Additionally, grassland bird selection of breeding territory is likely relative to residual vegetation from previous growing seasons, as most of the new growth initiates after grassland bird breeding territories have been established in the northern mixed-grass prairie (Davis, 2005).

Statistical Analyses

Community Composition. – We used the nonparametric Multi-Response Permutation Procedure (MRPP) to assess the effects of livestock grazing management on grassland bird community composition (Ahlering and Merkord, 2016). Multivariate analyses allow for the detection of patterns among many species within a community in relation to variables of interest, such as vegetation conditions or treatment effects (Conner and Adkisson, 1977). The MRPP evaluates differences among groups of entities and calculates a statistic of chance-corrected within-group agreement, *A* (Mielke 1984; 1991). The *A* statistic compares observed within-group homogeneity to that which is expected by chance, where $A = 0$ is the result expected at random. We randomly selected a number of survey sites per grazing system equal to the system with the fewest number of survey points [season-long] so sampling effort was equal, and selected the survey visit with the maximum count for each site. We then created a matrix of bird species by sites and used the Bray-Curtis distance measure (Bray and Curtis, 1957; Faith et al., 1987) within the MRPP to analyze grassland bird community composition among three grazing systems [season-long, summer-rotation, rest-rotation grazing] and among the three treatments within rest-rotation grazing systems [grazing during the growing season, grazing post-growing season, rest from grazing]. Six grassland-associated bird species (Table S1) had fewer than 5 total detections and were considered transients (non-breeders) and excluded from the community composition analyses (Hovick et al. 2015). We displayed grassland bird community separation among grazing systems and among rest-rotation treatments using Nonmetric Multi-Dimensional Scaling

(NMDS) ordinations (Kruskall, 1964; Minchin, 1987). Statistical analyses were conducted in program R (R Core Team, 2017). The MRPP and NMDS were conducted within R package 'vegan' (Oksanen et al., 2015). Figures were created using R package 'ggplot2' (Wickham, 2016).

Abundance. – We considered sets of competing models at 3 scales in our evaluation of livestock grazing on grassland bird abundance; local-, landscape-, and management-scale. We evaluated the effects of specific vegetation conditions on grassland bird abundance at the local-scale (within 100 m of the survey point) and landscape-scale (within 500 m and 1,000 m). Implementation of livestock grazing systems, manipulation of stocking rates, and evaluation of rangeland production potential within pastures are three main considerations of range managers on an annual basis, i.e. management-scale. We used R packages 'unmarked' (Fiske and Chandler, 2011) and 'AICcmodavg' (Mazerolle, 2013) to identify specific effects on abundance of each focal species using N-mixture abundance models (Royle, 2004). The N-mixture model simultaneously estimates detection probability (p) and abundance of unmarked individuals identified during spatially replicated counts within a closed survey period (Royle, 2004).

Based on hypothesized relationships for each covariate included in our models, we evaluated whether a linear, quadratic, or pseudo-threshold (pseudo-asymptotic) effect (Franklin et al., 2000) was best supported for its influence on avian detection probability or abundance. We then used stepwise model selection techniques to identify the variables influencing detection probability and abundance for each focal grassland bird species, starting with a highly parameterized model and eliminating uninformative parameters based on their lack of influence in the model, identified by lowest $|z|$ (Montgomery et al., 2012; Ahlering and Merkord, 2016). Variables considered to influence detection probability of grassland birds were Julian day, observer, shrub cover, shrub height, time of day, viewshed, wind speed, and year. Models evaluating detection probabilities of grassland birds were fit prior to fitting abundance models.

The vegetation conditions we measured in the field were previously shown to influence grassland bird detection probability or local abundance (Fisher and Davis, 2010; Ahlering and Merkord, 2016), and stepwise model selection was appropriate in the absence of any *a priori* hypotheses. Variables considered to influence abundance of grassland birds at the local-scale were bare ground cover, litter cover and depth, residual grass cover and height, shrub cover and height, wooded area, VOR, and the standard deviation of VOR (sdVOR) as a measurement of fine-scale heterogeneity in vegetation structure (Fisher and Davis, 2010; Thompson et al., 2014; Sliwinski et al., 2019). Litter cover and depth were correlated (Pearson's correlation estimate, $r > 0.6$), so we excluded litter cover from further analyses, as it may underestimate the true amount of litter available (Ricketts and Sandercock, 2016). Two variables were considered to influence abundance of grassland birds at the landscape-scale (500 m and 1000 m), wooded area and fence density (Sutter et al. 2000; Cunningham and Johnson, 2006; Thompson et al., 2014). Non-natural structures such as fence posts and fence lines can function as artificial perches in grassland landscapes and may attract some species of grassland birds (i.e., western meadowlark, vesper sparrow) to broadcast their songs during the breeding season (Sutter et al., 2000; Thompson et al. 2015). We did not include multiple spatial scales in a single model to avoid issues of multicollinearity (Thompson et al., 2014).

We used Akaike's Information Criterion adjusted for finite samples (AIC_c) to compare models and identify important variables to include in the final detection or abundance model for each grassland bird species. Supported models with large model weights (w_i) and AIC_c values ≤ 2 from the best-fit model were considered parsimonious (Burnham et al., 2011). When a supported model differed from the best-fit model by a single parameter, we considered the additional parameter to be uninformative (Arnold, 2010). We built a candidate model set for the management-scale effects on avian abundance based on *a priori* hypotheses, which included additive effects, along with 2- and 3-way interactions. Factors hypothesized to affect avian abundance at the management-scale were grazing system, stocking rate, and rangeland production potential.

We assessed model fit for the top model within local-, landscape-, and management-scale analyses for each focal species from 1,000 simulated datasets using the Nmix.gof.test function within R package 'AICcmodavg' (Mazerolle, 2013). Goodness-of-fit tests indicated $\hat{c}$ estimates between 0.75 and 1.0, and *P*-values > 0.95 for the most parsimonious models within each model set, providing strong evidence the models adequately fit the data. The best-fit model within our local-, landscape-, and management-scale analysis was then used to generate predictions of focal species abundance over the range of values for each variable, while holding other variables included in the best-fit model at their mean. When multiple models shared support (ΔAIC_c values ≤ 2), model averaged estimates were used to generate predictions of grassland bird detection probabilities and local abundance (Cade, 2015).

Habitat. – Vegetation metrics quantifying grassland bird habitat were summarized among grazing systems and among the three treatments within rest-rotation systems and evaluated using mixed effects analysis of variance (ANOVA). We used R package 'lme4' (Bates et al., 2012) to build models and included year and site as random effects to account for potential autocorrelation resulting from repeated measures at sites in 2016 and 2017 and because 15 vegetation plots were measured at each site (Sliwinski et al., 2019).

Results:

During 2016–17, we conducted 1,830 point-count surveys within eight pastures managed with cattle grazing and identified a total of 68 bird species, 31 of which were grassland-associated species (Table 21). We found that no grassland-associated species with >5 detections (non-transient) was unique to a single grazing system. Using the rarified subset of community data, we recorded 21 grassland-associated species in pastures within rest-rotation grazing systems, 24 species in two-pasture summer-rotation grazing systems, and 22 in season-long grazing systems. Grassland bird community separation among grazing systems was minimal, indicated by results from the MRPP and visualized by the NMDS ordination plot of species by site polygons representing the bird communities recorded within each grazing system (Fig. 18A). The MRPP indicated 2.0% of the variation in grassland bird community composition could be attributed to livestock grazing system (*A*: 0.020, $P < 0.001$). In addition, community composition was similar among the three types of grazing treatments within the rest-rotation system, where 0.4% of the variation in grassland bird communities can be attributed to the differences among these three treatments (*A*: 0.004, $P = 0.04$; Fig. 18B). Generally, the occurrences of Baird's sparrow (*Ammodramus bairdii*), bobolink (*Dolichonyx oryzivorus*), grasshopper sparrow, horned lark (*Eremophila alpestris*), Sprague's pipit (*Anthus spragueii*), upland sandpiper (*Bartramia* *longicauda*), and western meadowlark were associated, and this group tended to be dissociated with occurrences of clay-colored sparrow (*Spizella pallida*), eastern kingbird (*Tyrannus tyrannus*), field sparrow (*Spizella pusilla*), lark sparrow (*Chondestes grammacus*), loggerhead shrike (*Lanius ludovicianus*), mountain bluebird (*Sialia currucoides*), mourning dove (*Zenaida macroura*), and western kingbird (*Tyrannus verticalis*).

Table 21. Bird species observed during 2016 and 2017 avian point-count surveys at 610 sites on 8 pastures managed for livestock grazing in eastern Montana.

Common Name	Scientific Name	4-letter Code[a]
American Crow	*Corvus brachyrhynchos*	AMCR
American Goldfinch	*Carduelis tristis*	AMGO
American Kestrel*	*Falco sparverius*	AMKE
American Robin	*Turdus migratorius*	AMRO
American Widgeon	*Anas americana*	AMWI
Baird's Sparrow*	*Ammodramus bairdii*	BAIS
Bank Swallow	*Riparia riparia*	BANS
Baltimore Oriole	*Icterus galbula*	BAOR
Barn Swallow	*Hirundo rustica*	BARS
Black-billed Magpie	*Pica hudsonia*	BBMA
Belted Kingfisher	*Megaceryle alcyon*	BEKI
Brown-headed Cowbird	*Molothrus ater*	BHCO
Black-headed Grosbeak	*Pheucticus melanocephalus*	BHGR
Bobolink*	*Dolichonyx oryzivorus*	BOBO
Brewer's Blackbird	*Euphagus cyanocephalus*	BRBL
Brewer's Sparrow*	*Spizella breweri*	BRSP
Brown Thrasher	*Toxostoma rufum*	BRTH
Bullock's Oriole	*Icterus bullockii*	BUOR
Canada Goose	*Branta canadensis*	CAGO
Clay-colored Sparrow*	*Spizella pallida*	CCSP
Cedar Waxwing	*Bombycilla cedrorum*	CEDW
Chipping Sparrow	*Spizella passerina*	CHSP
Cliff Swallow	*Petrochelidon pyrrhonota*	CLSW
Common Grackle	*Quiscalus quiscula*	COGR
Common Nighthawk*	*Chordeiles minor*	CONI
Common Yellowthroat*	*Geothlypis trichas*	COYE
Eastern Bluebird*	*Sialia sialis*	EABL
Eastern Kingbird*	*Tyrannus tyrannus*	EAKI
European Starling	*Sturnus vulgaris*	EUST
Field Sparrow*	*Spizella pusilla*	FISP
Gray Catbird	*Dumetella carolinensis*	GRCA
Grasshopper Sparrow*	*Ammodramus savannarum*	GRSP

Hairy Woodpecker	*Leuconotopicus villosus*	HAWO
Horned Lark*	*Eremophila alpestris*	HOLA
House Wren	*Troglodytes aedon*	HOWR
Killdeer*	*Charadrius vociferus*	KILL
Lark Bunting	*Calamospiza melanocorys*	LARB
Lark Sparrow*	*Chondestes grammacus*	LASP
Least Flycatcher	*Empidonax minimus*	LEFL
Loggerhead Shrike*	*Lanius ludovicianus*	LOSH
Marbled Godwit*	*Limosa fedoa*	MAGO
Mallard	*Anas platyrhynchos*	MALL
Mountain Bluebird*	*Sialia currucoides*	MOBL
Mourning Dove*	*Zenaida macroura*	MODO
Northern Flicker	*Colaptes auratus*	NOFL
Northern Harrier*	*Circus hudsonius*	NOHA
Northern Rough-Winged Swallow	*Stelgidopteryx serripennis*	NRWS
Orchard Oriole	*Icterus spurius*	OROR
Prairie Falcon*	*Falco maxicanus*	PRFA
Ring-necked Pheasant*	*Phasianus colchicus*	RNEP
Rock Pigeon	*Columba livia*	ROPI
Rock Wren	*Salpinctes obsoletus*	ROWR
Red-tailed Hawk	*Buteo jamaicensis*	RTHA
Red-winged Blackbird*	*Agelaius phoeniceus*	RWBL
Say’s Phoebe*	*Sayornis saya*	SAPH
Sprague’s Pipit*	*Anthus spragueii*	SPPI*
Spotted Towhee	*Pipilo maculatus*	SPTO
Sharp-tailed Grouse*	*Tympanuchus phasianellus*	STGR
Tree Swallow	*Hirundo nigricans*	TRES
Upland Sandpiper*	*Bartramia longicauda*	UPSA
Vesper Sparrow*	*Pooecetes gramineus*	VESP
Western Kingbird*	*Tyrannus verticalis*	WEKI
Western Meadowlark*	*Sturnella neglecta*	WEME
Western Wood-Pewee	*Contopus sordidulus*	WEWP
Willow Flycatcher	*Empidonax traillii*	WIFL
Yellow-breasted Chat	*Icteria virens*	YBCH
Yellow-headed Blackbird*	*Xanthocephalus xanthocephalus*	YHBL
Yellow Warbler	*Dendroica petechia*	YWAR

* Indicates grassland associated speces

A 4-letter codes from the American Ornithological Society’s checklist of birds.

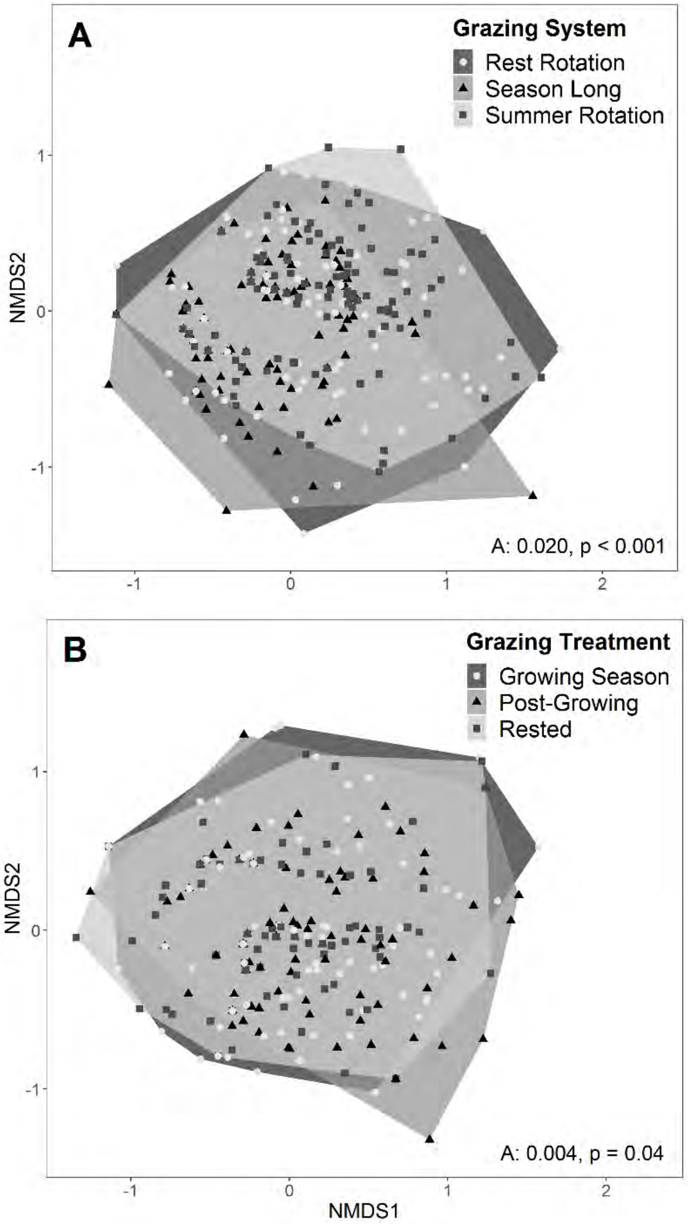

Figure 18. Grassland bird community composition among (A) grazing systems, and among (B) three treatments within rest-rotation grazing systems in eastern Montana, 2016–17. Scores from nonmetric multidimensional scaling (NMDS) analyses, representing relative distances among bird communities at each site in 2-diminsional ordination, are displayed as the x- and y-axis. Grayscale polygons represent the grassland bird communities associated with each of three grazing systems or treatments. The *A* statistic from the MRPP and significance of the test (*P*-value) are reported. (A) ●= sites within rest-rotation grazing systems, ▲ = sites within season-long grazing systems, and ■ = sites within summer-rotation grazing systems. (B) ● = sites within growing-season treatment, ▲ = sites within the post growing-season treatment, and ■ = sites within the rested treatment.

Grasshopper Sparrow. – The probability of detecting a grasshopper sparrow increased with viewshed ($\beta = 0.11 \pm 0.06$), decreased with time of day from 05:00 to 09:00 ($\beta = -0.27 \pm 0.06$; Tables 22, 25), and showed quadratic relationships with Julian day and shrub height, where the probability of detection was maximized during the middle of the survey season (~158th Julian day; 7 June) and at a shrub height of ~30 cm (Fig. 19). After accounting for detection probability, two models shared support ($\Delta AIC_c \leq 2$, $\Sigma w_i = 0.75$) for local-scale effects on grasshopper sparrow abundance (Table 22). Local abundance was maximized at approximately 10% bare ground cover, 15 cm residual grass height, and 3 cm litter depth, declined linearly with shrub height ($\beta = -0.8 \pm 0.03$), and showed a strong negative pseudo-asymptotic relationship with wooded area, where predicted abundance decreased dramatically beyond 0 % wooded ($\beta = -0.35 \pm 0.04$; Table 4, Fig. 4). A single model was supported for landscape-scale effects on grasshopper sparrows ($w_i = 0.96$; Table 23). Local abundance decreased sharply with increasing fence density ($\beta = -0.08 \pm 0.03$) within a 500-m^2 area of the survey point and decreased sharply when wooded area within a 1000-m^2 area of the point increased beyond 2 % (Fig. 20).

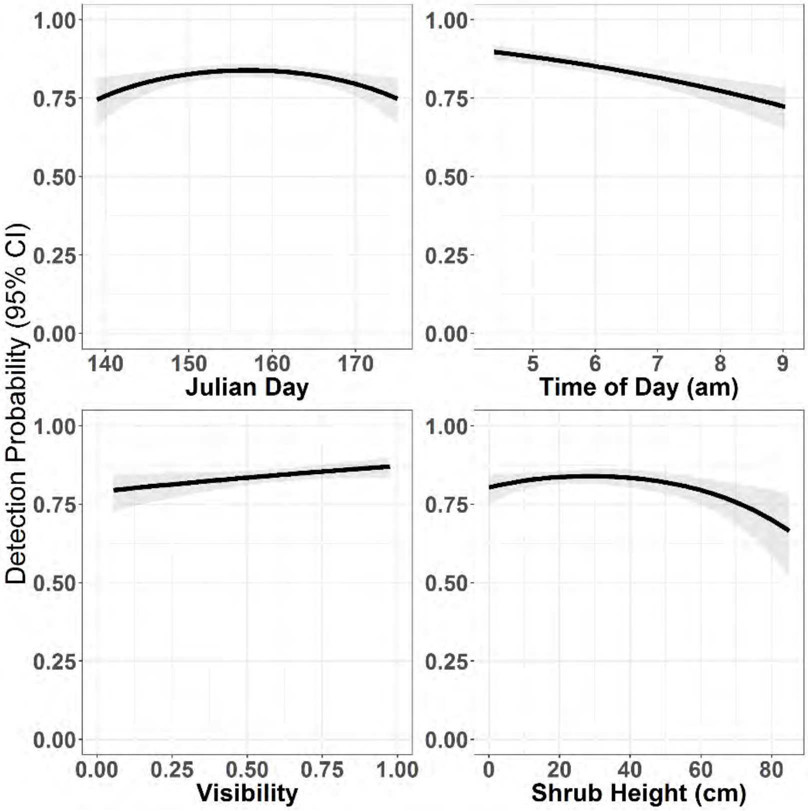

Figure 19. Predicted relationships for the effects of environmental or survey conditions on detection probability of grasshopper sparrow in eastern Montana, 2016–17.

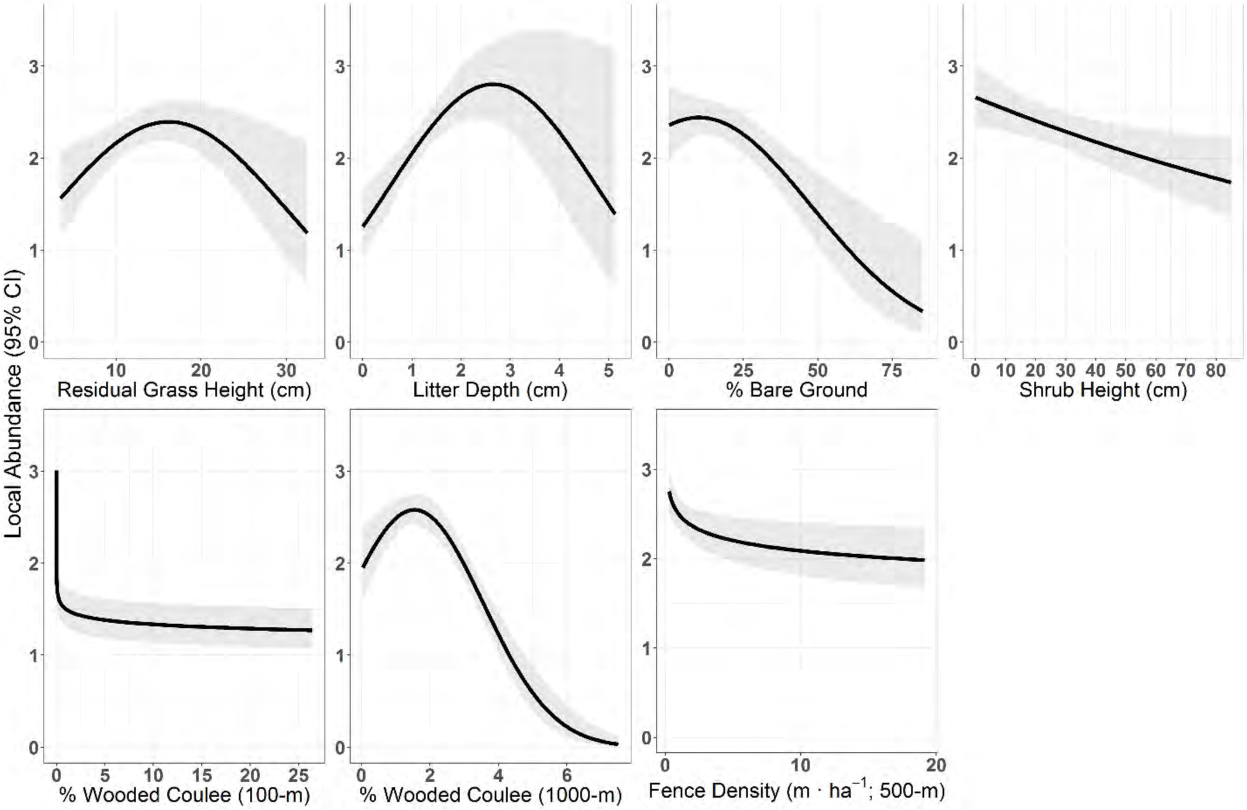

Figure 20. Predicted relationships between local- and landscape-scale habitat conditions and local abundance of grasshopper sparrow in eastern Montana, 2016–17.

A single model of grasshopper sparrow abundance at the management-scale had strong support ($w_i = 0.81$) and included an interaction between grazing system and rangeland production potential, as well as a negative effect of stocking rate (Table 24). Abundance was positively associated with rangeland production in season-long grazing systems ($\beta = 0.25 \pm 0.11$), while a quadratic relationship was supported in summer-rotation ($\beta_{productivity} + \beta_{productivity}{}^2 = 0.60$ (0.08SE) - 0.30 (0.08)) and rest-rotation grazing systems ($\beta_{productivity} + \beta_{productivity}{}^2 = 0.39$ (0.05) - 0.18 (0.03)), where predictions indicate abundance was maximized at intermediate values of rangeland production potential, from 1,700 – 2,000 kg · ha^{-1} (Table 25, Fig. 21A). Grasshopper sparrow abundance decreased with stocking rate ($\beta = -0.10 \pm 0.03$; Fig. 22), and the effect was similar among grazing systems.

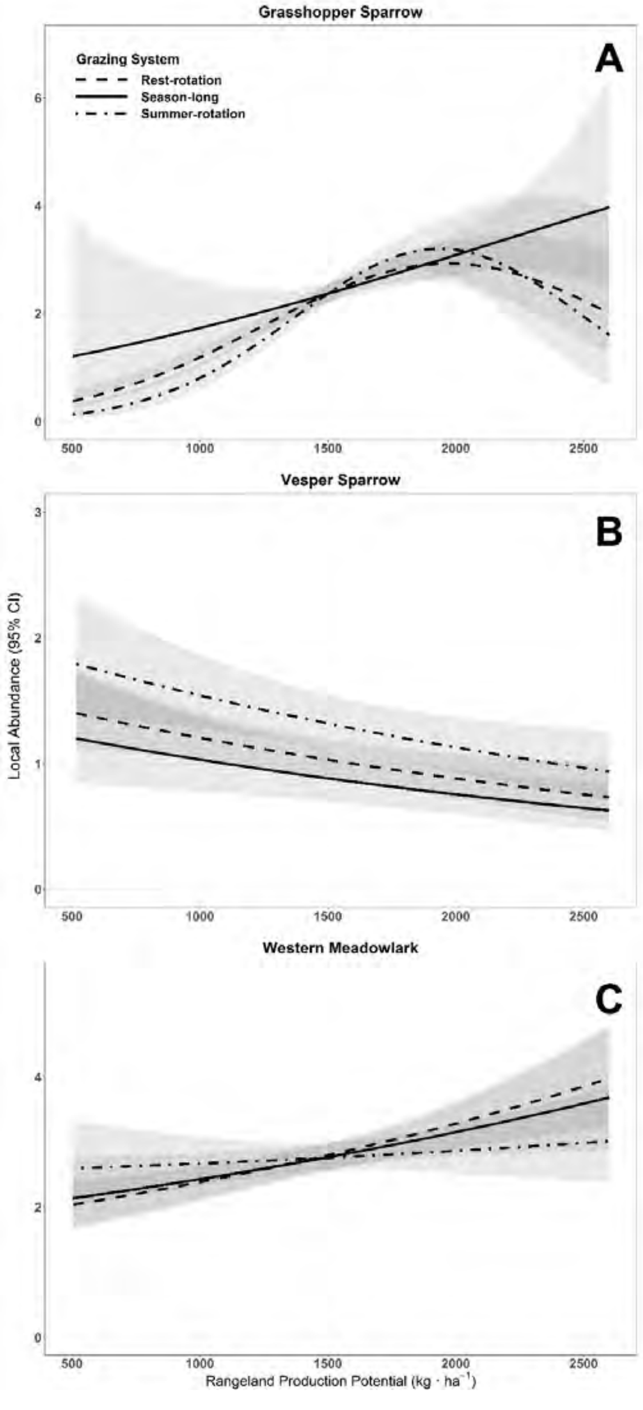

Figure 21. Relationships between rangeland production potential and predicted local abundance of (A) grasshopper sparrow, (B) vesper sparrow, and (C) western meadowlark among three grazing systems in eastern Montana, 2016–17.

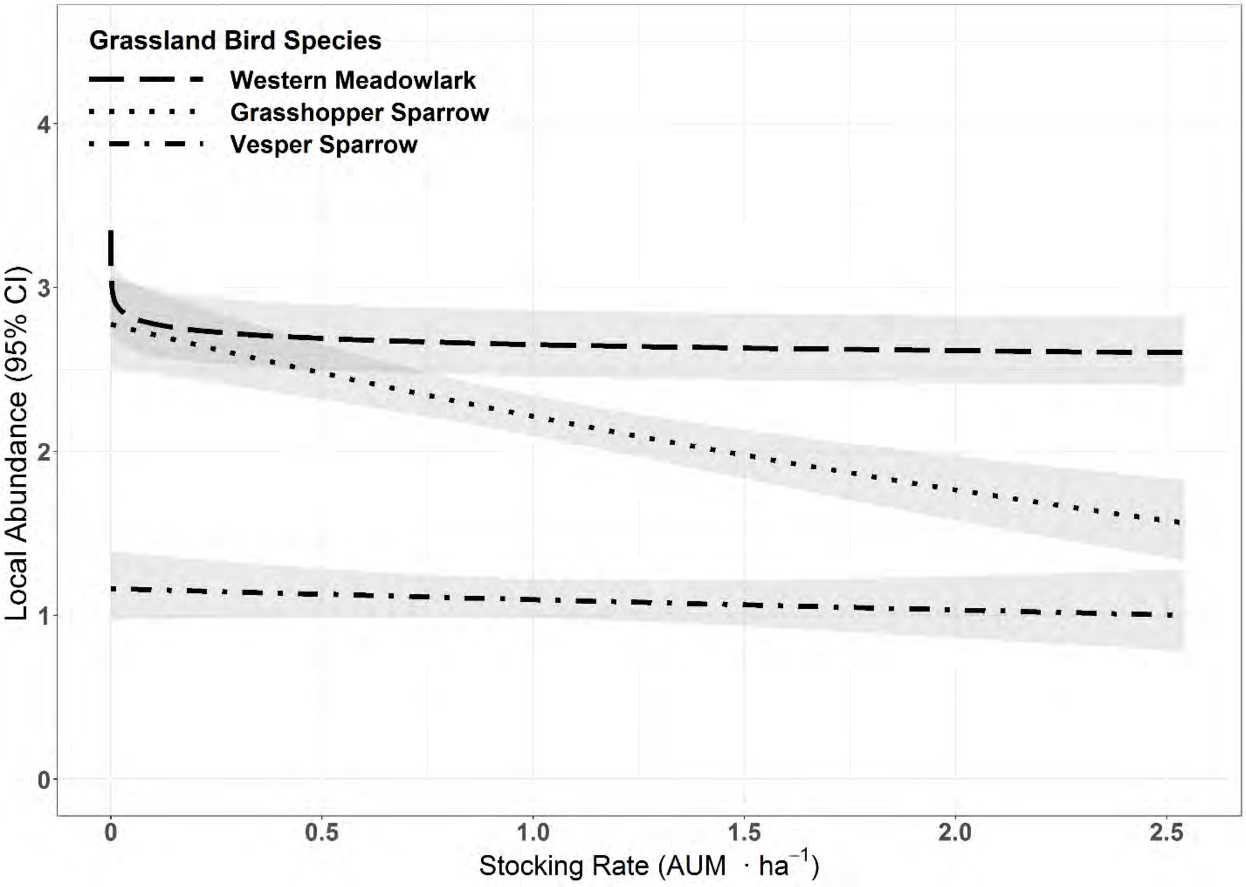

Figure 22. Relationships between stocking rate and predicted local abundance of three grassland bird species in eastern Montana, 2016-17.

Vesper Sparrow. – The probability of detecting a vesper sparrow was higher in 2017 than 2016 ($\beta = 0.50 \pm 0.14$), decreased with viewshed ($\beta = -0.19 \pm 0.07$) and wind speed ($\beta = -0.15 \pm 0.07$; Table 25), and exhibited a quadratic relationship with Julian day, where detection probability was lowest during the middle of the survey season (~ 4 June; Fig. 23). Four models shared support ($\Delta AIC_c \leq 2$) for local-scale effects on abundance of vesper sparrows (Table 22). Models including the main effects of bare ground, litter depth, shrub cover, and visual obstruction had the majority of support ($\Sigma w_i = 0.77$). Abundance increased with bare ground cover up to 75 % ($\beta = 0.16 \pm 0.06$) and litter depth up to 5 cm ($\beta = 0.11 \pm 0.05$), decreased with visual obstruction from 0 to 5 dm ($\beta = -0.11 \pm 0.05$), and showed a positive pseudo-asymptotic relationship to shrub cover, where abundance increased sharply from 0 – 5 % cover but was similar beyond 5 % ($\beta = 0.17 \pm 0.05$; Table 25, Fig. 24). Models including landscape-scale variables wooded coulee area and fence density shared support ($\Delta AIC_c \leq 2.0$; Table 23). Local abundance increased asymptotically with wooded area ($\beta = 0.15 \pm 0.05$) within 1,000-m^2 of the survey point, up to 6 % wooded (Fig. 24). Vesper sparrow abundance decreased with fence density ($\beta = -0.07 \pm 0.04$) within 1,000-m^2 area of the survey point.

Two models shared support ($\Delta AIC_c < 2.0$) for management-scale effects on vesper sparrow abundance (Table 24). The top-ranked model ($w_i = 0.59$) included main effects of grazing system and rangeland production potential, while the next top model ($w_i = 0.31$) included the additional main effect of stocking rate, a parameter that may be uninformative. Relative to rest-rotation grazing systems, abundance of vesper sparrow was higher in summer-rotation grazing systems ($\beta = 0.25 \pm 0.10$) and similar in season-long systems ($\beta = -0.17 \pm 0.14$; Table 25, Fig. 21B). Vesper sparrow abundance decreased with rangeland production potential at the study area from 500 – 2,500 kg · ha^{-1} ($\beta = -0.13 \pm 0.05$), and the effect was similar among grazing systems (Fig. 21B). A model that included a negative effect of stocking rate on abundance of vesper sparrows was supported ($\beta = -0.04 \pm 0.05$; Table 24), but the 95% confidence interval of the effect overlapped 0 (-0.13–0.05).

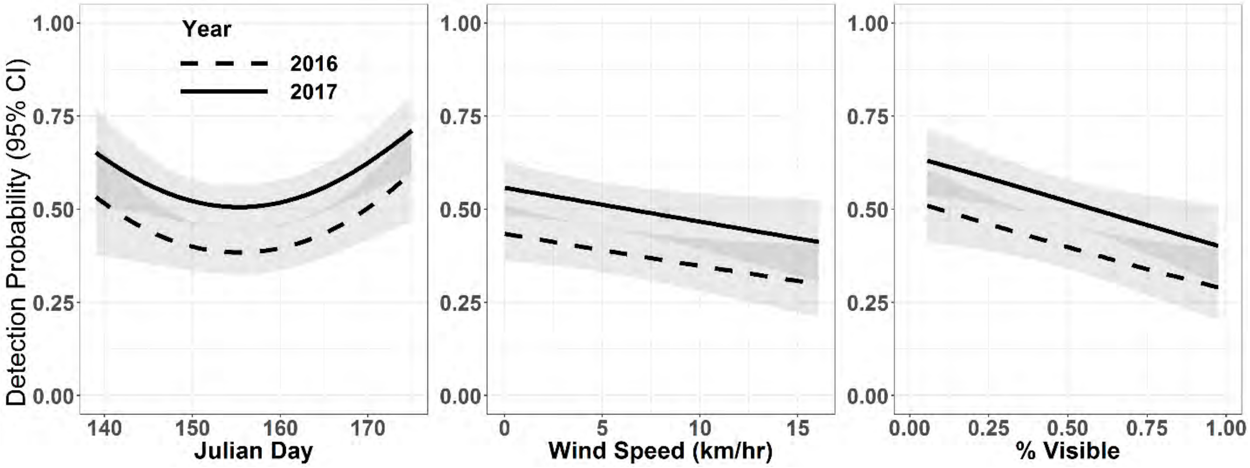

Figure 23. Predicted relationships for the effects of environmental or survey conditions on detection probability of vesper sparrow in eastern Montana, 2016–17.

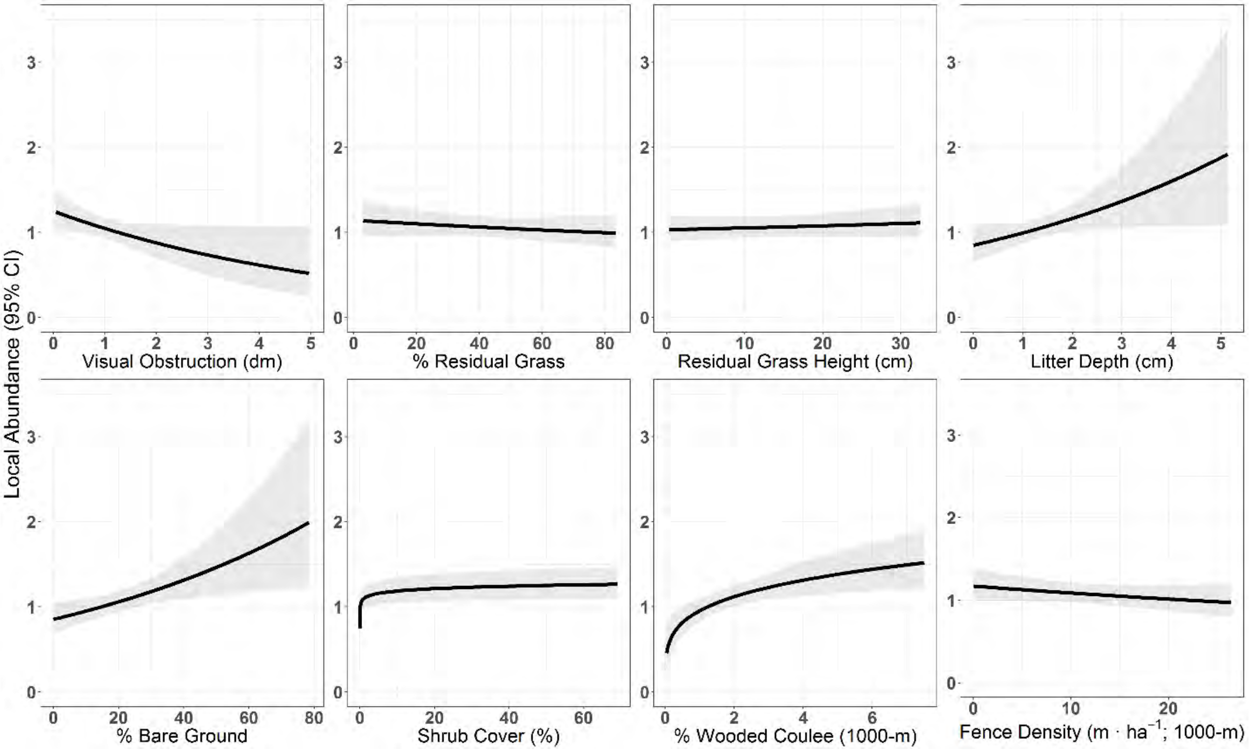

Figure 24. Predicted relationships between local- and landscape-scale habitat conditions and local abundance of vesper sparrow in eastern Montana, 2016–17.

Western Meadowlark. – The probability of detecting a western meadowlark was higher in 2017 than 2016 ($\beta = 0.37 \pm 0.11$), increased with viewshed ($\beta = 0.10 \pm 0.05$), and decreased with Julian day ($\beta = -0.32 \pm 0.05$) and wind speed ($\beta = -0.08 \pm 0.05$; Table 22, Fig. 25). Models that included the effects of visual obstruction, residual grass cover, forb cover, litter depth, and bare ground cover had the majority of support ($w_i = 0.73$) on local-scale abundance of western meadowlarks (Table 22). Abundance increased asymptotically with litter depth from 0 to 5 cm ($\beta = 0.22 \pm 0.05$) and forb cover from 0 to 50 % ($\beta = 0.09 \pm 0.03$) and decreased with visual obstruction from 0 – 5 dm ($\beta = -0.16 \pm 0.03$), residual grass cover from 0 to 80 % ($\beta = -0.11 \pm 0.04$), and bare ground cover from 0 to 75 % ($\beta = -0.09 \pm 0.04$; Table 25, Fig. 26). Abundance of western meadowlark decreased ($\beta = -0.06 \pm 0.03$) with increasing wooded area within 1000-m^2 area of the survey point from 0 to 7 % (Fig. 26).

Two models shared support ($\Delta AIC_c < 2.0$) for management-scale effects on western meadowlark abundance (Table 24). The top model included an interaction between grazing system and rangeland production potential, and a negative effect of stocking rate ($w_i = 0.60$). The data also supported a model that included main effects of rangeland production potential and stocking rate ($w_i = 0.31$). Model-averaged predictions show abundance of western meadowlark increased with rangeland production potential in season-long ($\beta = 0.11 \pm 0.06$) and rest-rotation grazing systems ($\beta = 0.15 \pm 0.04$; Fig. 21C), and declined sharply with stocking rate from 0 – 0.1 AUM · ha^{-1} ($\beta = -0.09 \pm 0.03$; Fig. 22; Table 25). Predictions from the two supported models estimate abundance of western meadowlark was highest in summer-rotation grazing systems in areas of relatively low production potential (<1,000 kg · ha^{-1}) and in season-long and rest-rotation systems in areas of relatively high production potential (>1,500 kg · ha^{-1}; Fig. 21C).

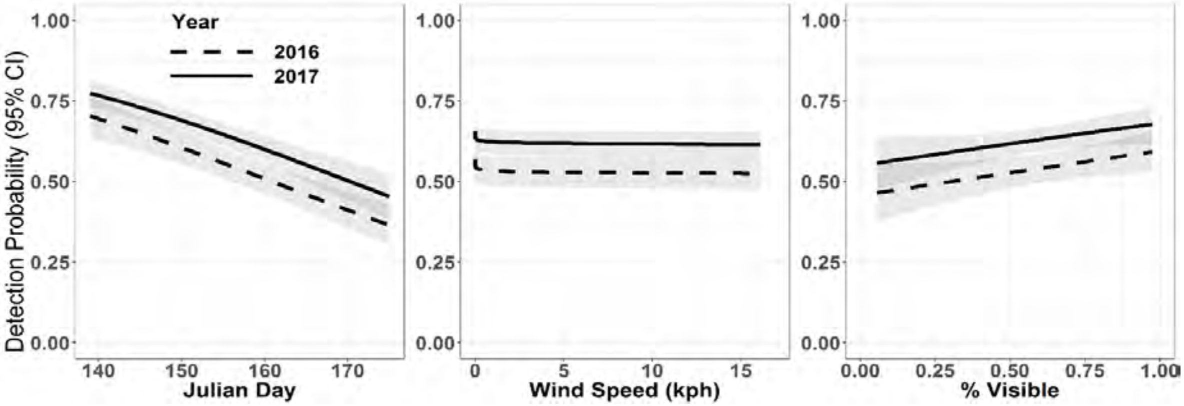

Figure 25. Predicted relationships for the effects of environmental or survey conditions on detection probability of western meadowlark in eastern Montana, 2016–17.

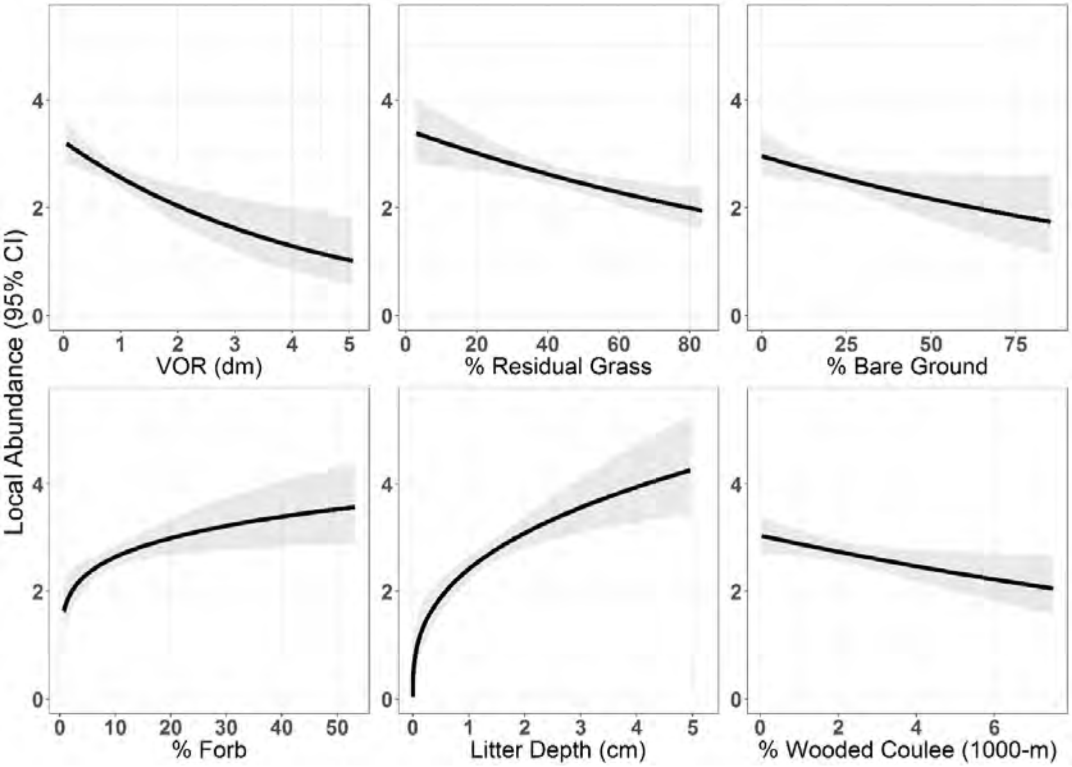

Figure 26. Predicted relationships between local- and landscape-scale habitat conditions and local abundance of western meadowlark in eastern Montana, 2016–17.

Table 22. Model selection results evaluating the effects of local-scale habitat conditions on abundance of grassland birds in eastern Montana, 2016–17.

Model[a]	K[b]	AIC$_c$	ΔAIC$_c$	w_i	$\sum w_i$
Grasshopper Sparrow					
$RH^2 + LD^2 + BG^2 + SH + \ln(WA)$[c]	16	4159.20	0.00	0.43	0.43
$RH^2 + LD^2 + BG^2 + SH + \ln(WA) + \ln(RC)$	17	4159.77	0.57	0.32	0.75
Constant (null)	2	4450.64	291.44	0.00	1.00
Vesper Sparrow					
VOR + Forb + LD + BG + ln(SC)	12	3025.45	0.00	0.28	0.28
VOR + Forb + LD + BG + ln(SC) + RH	13	3026.22	0.77	0.19	0.48
VOR + LD + BG + ln(SC)	11	3026.64	1.18	0.16	0.63
VOR + Forb + LD + BG + ln(SC) + RH + RC	14	3026.99	1.53	0.13	0.77
Constant (null)	2	3071.97	46.52	0.00	1.00
Western Meadowlark					
VOR + RC + ln(LD) + BG + ln(Forb)	11	4832.06	0.00	0.32	0.32
VOR + RC + ln(LD) + BG + ln(Forb) + RH + SC	13	4832.93	0.87	0.21	0.53
VOR + RC + ln(LD) + BG + ln(Forb) + SC	12	4833.01	0.95	0.20	0.73
Constant (null)	2	4965.84	133.77	0.00	1.00

[a] Only supported models with ΔAIC$_c$ values ≤ 2.0 and the null model are presented for each species.

[b] K = number of parameters.

[c] BG = Bare ground cover, Forb = Forb cover, LD = Litter depth, RC = Residual grass cover, RH = Residual grass height, SC = Shrub cover, SH = Shrub height, VOR = Visual obstruction reading, sdVOR = standard deviation of VOR, WA = Wooded coulee area, ^{2} = quadratic effect, ln() = pseudo-threshold effect.

Table 23. Model selection results evaluating the effects of landscape-scale habitat conditions on abundance of grassland birds in eastern Montana, 2016–17.

Model[a]	*K*[b]	AIC$_c$	ΔAIC$_c$	w_i	$\sum w_i$
Grasshopper Sparrow					
WA1000^2 + ln(FD500)[c]	12	4297.63	0.00	0.95	0.95
Constant (null)	9	4378.75	81.12	0.00	1.00
Vesper Sparrow					
ln(WA1000) + FD1000	8	3044.03	0.00	0.57	0.57
ln(WA1000)	7	3044.59	0.56	0.43	1.00
Constant (null)	6	3054.34	10.31	0.00	1.00
Western Meadowlark					
WA1000	7	4896.91	0.00	0.52	0.52
WA1000 + FD500	8	4898.41	1.49	0.24	0.76
Constant (null)	6	4898.46	1.55	0.24	1.00

[a] Only supported models with ΔAIC$_c$ values ≤ 2.0 and the null model are presented for each species.

[b] *K* = number of parameters.

[c] FD500 = Fence density at the 500 m spatial scale, FD1000 = Fence density at the 1,000 m scale, WA500 = Wooded area at the 500 m scale, WA1000 = Wooded area at the 1,000 m scale, ^{2} = quadratic effect, ln() = pseudo-threshold effect.

Table 24. Model selection results evaluating the management-scale effects of grazing system, stocking rate, and rangeland production potential on grassland bird abundance in eastern Montana, 2016–17.

Model[a]	K[b]	AIC_c	ΔAIC_c	w_i	$\sum w_i$
Grasshopper Sparrow					
GS × RPP^2 + SR[c]	15	4179.33	0.00	0.81	0.81
RPP^2 + SR	11	4183.35	4.02	0.11	0.92
GS + RPP^2 + SR	13	4184.75	5.42	0.05	0.97
GS × SR + RPP^2	13	4186.20	6.87	0.03	1.00
Constant (null)	8	4420.10	240.77	0.00	1.00
Vesper Sparrow					
GS + RPP	10	3034.13	0.00	0.59	0.59
GS + RPP + SR	11	3035.44	1.31	0.31	0.90
GS	9	3039.80	5.67	0.04	0.94
RPP	8	3041.30	7.17	0.02	0.96
Constant (null)	7	3049.63	15.50	0.00	1.00
Western Meadowlark					
GS × RPP + ln(SR)	12	4879.37	0.00	0.60	0.60
RPP + ln(SR)	10	4880.72	1.35	0.31	0.91
GS + RPP + ln(SR)	12	4885.32	3.91	0.08	0.91
GS × ln(SR) + RPP	12	4885.36	3.95	0.08	0.99
Constant (null)	6	4903.97	22.56	0.00	1.00

[a] Only models with AIC_c weights (w_i) > 0.01 and the null model are presented for each species.

[b] K = number of parameters.

[c] GS = Grazing system, RPP = Rangeland production potential, SR = Stocking rate, ^{2} = quadratic effect, ln() = pseudo-threshold effect.

Table 25. Effects of standardized local habitat, landscape-scale habitat, and management-scale variables on the abundance of three focal species in eastern Montana, 2016–17. Also included are the effects of year, Julian day, time of day, shrub height, and wind speed on probability of detection. [a, b]

	Grasshopper Sparrow		Vesper Sparrow		Western Meadowlark	
	β	SE	*β*	SE	*β*	SE
Detection[c]						
Intercept	**1.65**	0.08	**-0.46**	0.13	0.13	0.09
Year, 2017			**0.50**	0.14	**0.37**	0.11
Day	0.01	0.05	0.08	0.07	**-0.32**	0.05
Day^2	**-0.12**	0.04	**0.16**	0.06		
Time	**-0.27**	0.06				
Viewshed	0.11	0.06	**-0.19**	0.07	**0.10**	0.05
Shrub height	0.04	0.07				
Shrub height^2	**-0.08**	0.03				
Wind speed			**-0.15**	0.07		
ln(Wind speed)					-0.08	0.05
Abundance, local habitat						
Intercept	**0.86**	0.04	0.06	0.06	**0.96**	0.04
Residual grass cover					**-0.11**	0.04
Residual grass height	0.06	0.04				
Residual grass height^2	**-0.06**	0.02				
Litter depth	**0.20**	0.04	**0.11**	0.05		
Litter depth^2	**-0.05**	0.02				
ln(Litter depth)					**0.22**	0.05
Bare ground	**-0.10**	0.04	**0.16**	0.06	**-0.09**	0.04
Bare ground^2	**-0.07**	0.03				
Shrub height	**-0.08**	0.03				
ln(Wooded coulee)	**-0.35**	0.04				
VOR			**-0.11**	0.05	**-0.16**	0.03
Forb			0.08	0.04		
ln(Forb)					**0.09**	0.03
ln(Shrub cover)			**0.17**	0.05		
Abundance, landscape						
Intercept	**0.92**	0.04	0.07	0.06	**1.00**	0.04
Wooded coulee (1000 m)	**-0.15**	0.04			**-0.06**	0.03
Wooded coulee^2 (1000 m)	**-0.18**	0.04				
ln(Wooded coulee; 1000 m)			**0.15**	0.05		
Fence density (1000 m)			-0.07	0.04		
ln(Fence density; 500 m)	**-0.08**	0.03				

Table 25. continued

	Grasshopper Sparrow		Vesper Sparrow		Western Meadowlark	
	β	SE	*β*	SE	*β*	SE
Abundance, management						
Intercept	**0.86**	0.04	0.03	0.07	**1.02**	0.04
Season-long GS			-0.17	0.14		
Summer-rotation GS			**0.25**	0.10		
Stocking rate	**-0.10**	0.03				
ln(Stocking rate)					**-0.09**	0.03
RPP			**-0.13**	0.05		
Season-long GS × RPP	**0.25**	0.11			0.11	0.06
Season-long GS × RPP^2	-0.02	0.07				
Summer-rotation GS × RPP	**0.60**	0.08			-0.01	0.06
Summer-rotation GS × RPP^2	**-0.30**	0.08				
Rest-rotation GS × RPP	**0.39**	0.05			**0.15**	0.04
Rest-rotation GS × RPP^2	**-0.18**	0.03				

[a] Abundance covariates are presented on the log-scale and detection covariates on the logit scale.

[b] Bold numbers indicate the 95% confidence intervals did not overlap 0.

[c] GS = Grazing system, RPP = Rangeland production potential, SR = Stocking rate, VOR = Visual obstruction reading, ^{2} = quadratic effect, ln() = pseudo-threshold effect.

Habitat. – We analyzed the local habitat metrics collected at 9,150 plots within 610 bird survey areas among the three grazing systems, in addition to landscape-scale metrics wooded coulee area and fence density for each survey point. Several habitat components differed among grazing systems, including residual grass cover (*P* < 0.01), forb cover (*P* = 0.08), litter depth (*P* < 0.01), bare ground cover (*P* < 0.01), and shrub cover (*P* = 0.01) and height (*P* < 0.01; Table 26). On average, plots in season-long grazing systems had the highest (x̄ ± SE) residual grass cover (47.6 % ± 1.5), residual grass height (16.3 cm ± 0.67), litter depth (1.6 cm ± 0.07), and the lowest shrub cover (3.5 % ± 0.57) and height (18.5 cm ± 1.2). Plots in pastures managed with rest-rotation grazing had greater bare ground cover (22.4 % ± 0.81) and lower residual grass cover (37.7 % ± 0.93) and litter depth (1.3 cm ± 0.04), on average. Rest-rotation systems also included greater forb cover (11.0 % ± 0.32) relative to other systems (Table 26). Fence density at 500-m and 1,000-m scales was highest for sites within rest-rotation pastures, at 10.5 (± 0.41) and 12.9 (± 0.24) m · ha^{-1}, respectively. Generally, residual grass cover and litter depth were greater in 2017, and VOR, residual grass height, and forb cover were greater in 2016 (Table 27).

Several local vegetation components differed among treatments within rest-rotation systems, including residual grass cover (*P* < 0.01), residual grass height (*P* < 0.01), litter depth (*P* < 0.01), and bare ground cover (*P* < 0.01; Table 28). Residual grass height (15.8 cm ± 0.34) and litter depth (1.6 cm ± 0.08) were highest and bare ground cover was lowest (18.3 % ± 1.2) in the pastures rested from grazing the previous year. Residual grass cover was lowest in post-growing season treatments (32.5 % ± 1.3), and similar between growing-season (40.3 cm ± 1.9) and rested treatments (39.9 cm ± 1.5).

Table 26. Habitat metrics among three grazing systems in eastern Montana, 2016–17. Mean, standard error, minimum and maximum values presented for each variable. *P*-values reported for ANOVA on mixed-effects and generalized linear models among the three grazing systems.

	Season-long (n = 120)				Rest-rotation (n = 300)				Summer-rotation (n = 190)				ANOVA[a]
	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	*P*-value
VOR (dm)	0.92	0.05	0.0	2.5	0.90	0.04	0.07	5.0	0.95	0.04	0.07	5.1	0.74
Standard deviation VOR	0.61	0.04	0.0	3.4	0.75	0.04	0.18	4.6	0.72	0.04	0.18	4.6	0.22
Residual grass cover (%)	47.6	1.5	8.3	83.5	37.7	0.93	3.0	81.2	42.1	1.2	3.3	81.3	<0.01
Residual grass height (cm)	14.4	0.47	3.5	32.5	13.3	0.26	3.5	30.9	13.7	0.31	4.7	26.1	0.20
Forb cover (%)	10.3	0.38	1.3	19.3	11.0	0.32	1.8	53.2	9.8	0.32	0.67	26.3	0.08
Litter depth (cm)	1.6	0.07	0.40	4.3	1.3	0.04	0.0	5.1	1.4	0.05	0.23	3.4	<0.01
Bare ground cover (%)	15.5	1.1	0.0	71.2	22.4	0.81	0.33	85.3	19.8	0.96	0.17	68.8	<0.01
Shrub cover (%)	3.5	0.57	0.0	48.5	6.4	0.55	0.0	69.0	6.2	0.62	0.0	44.8	0.01
Shrub height (cm)	18.5	1.2	0.0	59.3	25.2	0.95	0.0	85.0	26.5	1.1	0.0	76.7	<0.01
% Wooded coulee (100-m)	0.52	0.21	0.0	16.9	1.8	0.25	0.0	26.3	1.9	0.33	0.0	24.5	0.01
% Wooded coulee (500-m)	0.81	0.10	0.0	4.5	2.0	0.09	0.0	6.9	2.4	0.14	0.0	11.1	<0.01
% Wooded coulee (1000-m)	1.4	0.08	0.04	3.7	2.0	0.06	0.52	4.8	2.6	0.10	0.89	7.5	<0.01
Fence density (m · ha^{-1}; 500-m)	6.3	0.60	0.0	22.1	10.5	0.41	0.0	30.3	8.3	0.53	0.0	28.4	<0.01
Fence density (m · ha^{-1}; 1000-m)	8.7	0.36	0.0	20.0	12.9	0.24	4.8	26.4	9.4	0.39	0.0	17.9	<0.01
Rangeland production potential (kg · ha^{-1})	1789	29	1027	2608	1372	27	197	2625	1518	26	616	2389	<0.01

[a] Analysis of Variance on mixed-effects and generalized linear models. Cover variables were logit transformed prior to analysis.

Table 27. Habitat metrics among three grazing systems by year in eastern Montana, 2016–17. Mean and standard error are presented for each variable.

	Season-long (n = 120)				Rest-rotation (n = 300)				Summer-rotation (n = 190)			
	2016		2017		2016		2017		2016		2017	
	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE
VOR (dm)	1.22	0.06	0.61	0.05	1.15	0.05	0.66	0.06	1.28	0.07	0.62	0.04
Standard deviation VOR	0.68	0.06	0.55	0.06	0.78	0.05	0.73	0.06	0.79	0.07	0.66	0.05
Residual grass cover (%)	42.5	1.99	52.8	1.98	32.2	1.23	43.2	1.25	38.3	1.78	45.8	1.59
Residual grass height (cm)	16.3	0.67	12.4	0.55	14.6	0.37	12.1	0.35	14.6	0.45	12.7	0.43
Forb cover (%)	10.8	0.49	9.91	0.56	11.5	0.49	10.6	0.40	10.4	0.48	9.21	0.43
Litter depth (cm)	1.46	0.12	1.71	0.06	1.10	0.06	1.58	0.04	1.12	0.06	1.74	0.06
Bare ground cover (%)	15.9	1.76	15.2	1.39	22.5	1.18	22.2	1.11	21.1	1.62	18.6	1.11

Table 28. Habitat metrics among the three treatments within rest-rotation grazing systems in eastern Montana, 2016–17. Mean, standard error, minimum and maximum values presented for each variable. *P*-values reported for ANOVA on mixed-effects and generalized linear models among the three treatments.

	Growing Season (n = 102)				Post Seed-ripe (n = 96)				Rested (n = 102)				ANOVA[a]
	x̄	SE	Min	Max	x̄	SE	Min	Max	x̄	SE	Min	Max	*P*-value
VOR (dm)	0.80	0.06	0.07	5.0	0.94	0.08	0.07	4.3	0.98	0.04	0.10	3.1	0.15
Standard deviation VOR	0.75	0.08	0.18	4.6	0.84	0.08	0.18	4.3	0.67	0.05	0.18	3.3	0.34
Residual grass cover (%)	40.3	1.9	3.0	81.2	32.5	1.3	9.7	71.2	39.9	1.5	7.5	74.5	<0.01
Residual grass height (cm)	12.4	0.42	5.0	30.9	11.8	0.50	3.5	24.5	15.8	0.34	6.7	25.5	<0.01
Forb cover (%)	10.9	0.69	2.2	53.2	10.7	0.46	2.0	21.0	11.5	0.45	1.8	24.2	0.54
Litter depth (cm)	1.3	0.06	0.0	3.1	1.2	0.06	0.45	4.2	1.6	0.08	0.33	5.1	<0.01
Bare ground cover (%)	24.7	1.5	0.50	85.3	24.2	1.4	1.3	72.0	18.3	1.2	0.33	70.7	0.01

[a] Analysis of Variance on mixed-effects and generalized linear models. Cover variables were logit transformed prior to analysis.

Objective 3b: Effects of livestock grazing management on mesocarnivore space use

Methods

Field sampling. – We collected data during two summer field seasons (May – July, 2016–17). Using ArcGIS (ESRI 2011, v10.1), We randomly generated 180 camera trap survey sites (90 each season) across gradients of habitat conditions within a Montana FWP Upland Gamebird Enhancement Program project managed under rest-rotation grazing, and on adjacent private and federal lands managed under season-long or 2-pasture summer-rotation grazing systems (Table 29, Figure 27). Within the 3-pasture rest-rotation grazing systems in the study area, cattle were turned out to the first pasture in late May, moved to the second pasture mid-August, and turned in after grazing the second pasture for 8–10 weeks; the third pasture in the system was rested from grazing. Season-long grazing systems in my study area allowed cattle to graze continuously from May or early June through October or mid-November. Within 2-pasture summer-rotation grazing systems in the study area, cattle were turned out to the first pasture in early June, moved to the second pasture after 6 – 8 weeks, and turned in for the season in early November. The summer-rotation grazing systems stocked cattle in the same pastures each year during approximately the same period of the summer grazing season. This is unlike typical 2-pasture deferred-rotation grazing systems, where pastures are not grazed during the same period of the summer grazing season in consecutive years.

Table 29. Pastures of study, size, and number of camera trap sites in eastern Montana during 2016–17.

Pasture[1]	**Grazing System**	**Size (ha)**	**Camera Traps[2]**
Rest.Ro1	Rest-rotation	1,169	31
Rest.Ro2	Rest-rotation	1,107	29
Rest.Ro3	Rest-rotation	730	20
Summ.Ro1	2-Pasture Summer-rotation	550	12
Summ.Ro2	2-Pasture Summer-rotation	1,908	26
Summ.Ro3	2-Pasture Summer-rotation	277	8
Se.Long1	Season-long	856	26
Se.Long2	Season-long	413	12

[1] Pasture locations within the study area are displayed in Appendix A, Figure A1.

[2] Of 180 camera trap sites surveyed, 16 were censored from analyses.

We deployed one passive infrared remote field camera (Browning BTC 5HD, Browning, Morgan, UT) at each of 90 camera trap sites during three sampling sessions in 2016 and 2017 (Table 29). Thus, 30 remote cameras were used to survey 180 sites during two field seasons. Sampling sessions ranged from 20 – 25 days (Table 30), and one sampling occasion was defined as a 5-day (120 hour) period. Partial sampling days (days of camera installation or removal) were excluded from sampling periods.

Table 30. Sampling periods for mesocarnivore camera trapping in eastern Montana during 2016–17.

Year	**Sampling Period**	**Date Range**[1]
2016	1	134 – 158
2016	2	160 – 179
2016	3	182 – 201
2017	1	139 – 163
2017	2	165 – 184
2017	3	186 – 205

[1] Julian day (1 – 365).

To maximize mesocarnivore detections, camera traps were set in the most optimal location within 200 m of the site, often areas along habitat edges where predators typically prefer to hunt and forage (Andrén 1995), or along game trails. Camera traps were spaced > 250 m apart to satisfy the assumption of site independence (Lesmeister et al. 2015). However, selection for the most optimal camera trap location within 200 m of the site unknowingly resulted in 20 camera traps set < 250 m from another camera trap. Of these, 8 were spaced 200 – 250 m apart and included in analyses, while 12 were less than 200 m apart and censored from analyses. Additionally, 4 camera trap sites were censored due to camera malfunction (2), cattle destruction (1), or theft (1). Of 180 original camera sites, 164 sites were used in analyses.

Due to the relatively small size of my study area (~7,000 ha), and the large home range of some mesocarnivores (coyote, summer range > 1,500 ha; Gosselink et al. 2003), the assumption of spatial independence of camera sites may be violated. As such, the definition of occupancy in my study is not necessarily true occupancy, but rather habitat use of mesocarnivores, as defined by Krausman (1999). Habitat use is a relevant and informative metric, as my main objective for this aspect of the study is to evaluate the influence of livestock grazing management on mesocarnivore use. This definition of occupancy will allow comparison among grazing systems in terms of mesocarnivore habitat use.

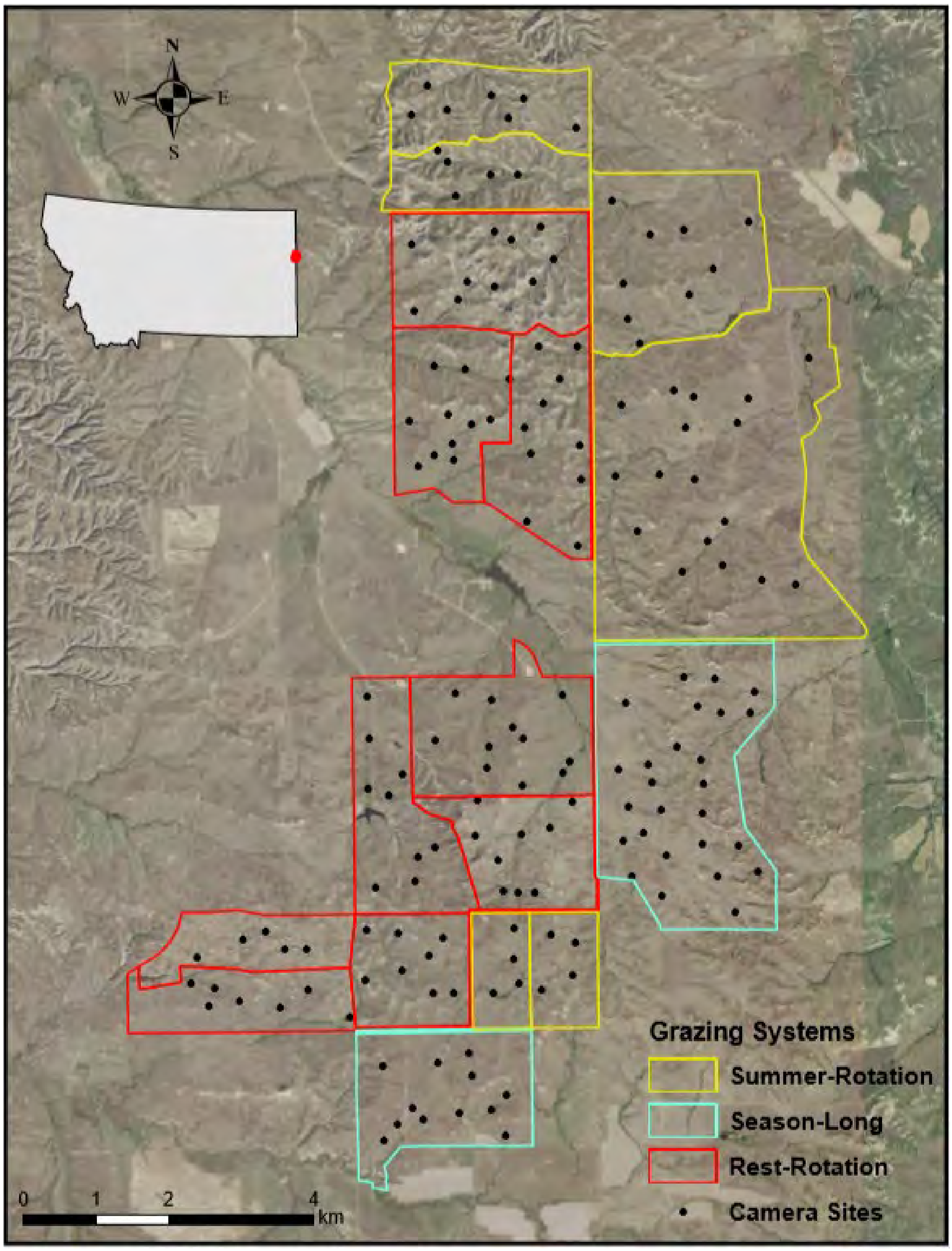

Figure 27. Study area in Richland County, Montana and McKenzie County, North Dakota, USA during 2016–17. Camera trap sites within pastures on the Montana FWP Upland Gamebird Enhancement Program project managed in a rest-rotation grazing system, and on adjacent pastures managed in season-long or summer-rotation grazing systems.

Cameras were programmed to be active 24 hours per day, with a two-photo burst for each photographic event and a 1-minute delay between events. Cameras were motion-activated, so a photographic event occurred when the remote camera was triggered by the presence of a mesocarnivore. Date, time, and camera identity were recorded by the camera for each photographic event. Cameras were secured to tree trunks or mounted on metal stakes and positioned approximately 0.5 m above the ground. When present, cameras were faced toward game trails to maximize detections. The area in front of each camera was cleared of obstructive vegetation, and a scent or bait lure was placed 2 m in front of the camera. Lures were used to increase mesocarnivore detections, and in 2016, consisted of a combination of fatty acid scent disks (U.S. Department of Agriculture Pocatello Supply Depot, Pocatello, ID), trapping lure (Gusto; Minnesota Trapline Products, Inc., Pennock, MN), and/or sardines. Only trapping lure was used in 2017. All camera sites during each sampling period received the same lure. During each sampling period, camera sites were revisited weekly to replenish lures, swap memory cards, change camera batteries, and remove any new obstructive vegetation.

Habitat Evaluation. – The study area was a contiguous, native grassland managed for livestock grazing, resulting in relatively few areas of common edge habitats, with which mesocarnivores are typically associated. We identified 5 potential habitat edges within the study site: wooded coulees, roads and two-tracks, pasture fences, water features, and oil pads. We used ArcMap 10.4 to digitize each of these features within the study site using five band 1-m resolution aerial imagery from the National Agricultural Imagery Program (NAIP) developed by the U.S. Farm Service Agency (ESRI 2011, v10.4). Data was obtained from Montana State Library GIS Clearinghouse and North Dakota GIS Hub Data Portal. We merged each of these features into a single ‘edge’ layer, and intersected this layer with buffered camera sites at 100-m, 500-m, and 1,000-m radial areas for analyses at multiple spatial scales (ESRI 2011, v10.4). We used the ArcMap ‘Calculate Geometry’ tool to estimate the total length of edge habitat associated at camera sites, and calculated edge density by dividing edge length by area at each of 100-m, 500-m, and 1,000-m spatial scales (ESRI 2011, v10.4). We used the ArcMap ‘Near’ tool to estimate the distance from each camera site to the nearest wooded coulee, pasture fence, road or two-track, water feature, or oil pad (ESRI 2011, v10.4).

Rangeland managers implement grazing systems based on the expected annual vegetative production of rangelands in an average year. We quantified rangeland production potential associated with each camera trap site using the Soil Survey Geographic database (SSURGO) ecological site data from the Natural Resources Conservation Service (NRCS) Web Soil Survey (NRCS 2017). NRCS defines rangeland production as “the amount of vegetation that can be expected to grow annually in a well-managed area that is supporting the potential natural plant community” (NRCS 2017). Previous researchers have found NRCS estimates of rangeland production potential based on the SSURGO ecological site data were reasonable estimates of true average rangeland productivity (Relyea et al. 2000). We calculated the weighted average rangeland production potential within 100 m of each camera trap site using the representative values (RV) of rangeland production for each ecological site type in the study area (Table 31), effectively accounting for camera trap sites which encompassed multiple ecological sites. We used the representative values of rangeland production potential, as precipitation during the years prior to field work was approximately average.

Table 31. Total areas of each ecological site and associated values of rangeland production potential on 8 pastures in eastern Montana and western North Dakota during 2016–17. Representative values of production potential are based on Soil Survey Geographic Database (SSURGO) ecological site data from the Natural Resources Conservation Service (NRCS) Web Soil Survey.

Ecological Site Description	**Representative Value**[1]	**Total Area**[2]
Wetland	6613	0.08
Wet Meadow	3923	0.25
Loamy Overflow	3587	47.38
Sandy Terrace	3363	1.56
Loamy Terrace	3250	22.93
Saline Lowland	2802	14.70
Sands	2802	86.27
Closed Depression	2690	0.05
Loamy	2690	688.0
Sandy	2690	114.48
Clayey	2130	132.08
Limy Sands	2018	6.44
Limy Residual	1905	1817.25
Claypan	1681	87.40
Shallow Loamy	1569	1189.01
Shallow Sandy	1569	32.59
Clayey-Steep	1233	588.33
Thin Loamy	1121	125.16
Shallow Clayey	1009	24.36
Badlands Fan	897	1119.20
Thin Claypan	897	27.19
Very Shallow	897	160.01
Badland	0	402.67
Non-site[3]	0	20.95
Rock Outcrop	0	17.73

[1] Representative Value (RV) defined as the rangeland production (kg · ha^{-1}) during a year with average precipitation.

[2] Total area (hectares) of each ecological site and associated value of rangeland production potential within the study area.

[3] Open water classified as Non-site.

We interviewed landowners to gather cattle turn-out/turn-in dates and number of head stocked to calculate stocking rates for the pastures within my study area. These dates and numbers were validated by observation of when and approximately how many cattle were present in pastures during both grazing seasons. We calculated stocking rates within pastures based on an animal unit month (AUM), the amount of forage, measured on a dry weight basis, to feed a 1,000-lb cow-calf pair for a 30-day period (Holechek et al. 2011). The average cow-calf pair grazing on the pastures within the study area was approximately 1,400 lbs (635 kg) based on landowner interviews, so we accounted for this in our calculations of stocking rate. Typically, stocking rates consider all pastures within a multi-pasture grazing system, resulting in a single stocking rate for the system. We calculated the stocking rates of each individual pasture within the 3-pasture rest-rotation and 2-pasture summer-rotation grazing systems because we were interested in the indirect effects of livestock grazing on mesocarnivore occupancy through livestock alteration of vegetation structure. Stocking rates from the previous year's grazing season were used as a predictor of mesocarnivore occupancy, as residual vegetation from the previous year's grazing establishes habitat structure used by mesocarnivores for hunting and foraging activities during the grassland bird breeding season when we conducted camera trap surveys.

Statistical Analyses. – We evaluated the effects of edge density (100-m, 500-m, and 1,000-m scale) and distance to the nearest wooded coulee, road, fence, water, and oil pad on mesocarnivore occupancy. We also evaluated the management-level effects of rangeland production potential (100-m scale), stocking rate, and grazing system on mesocarnivore occupancy. The habitat variables were considered for their direct effect on mesocarnivore occupancy through habitat use, whereas the three management-level variables were considered for their indirect effect on mesocarnivore occupancy through the ability of livestock grazing to alter vegetation structure within rangelands. Rangeland production potential is included in the management-level model set because range managers consider the average production potential of rangelands when implementing grazing systems or manipulating livestock stocking rates.

We conducted all analyses in program R (R Core Team 2016) with use of packages 'unmarked' (Fiske and Chandler 2011) and 'AICcmodavg' (Mazerolle 2013) to identify specific effects on occupancy of mesocarnivores, where single-season occupancy modeling allowed for simultaneous estimation of detection probability and occupancy (MacKenzie et al. 2006). Accounting for imperfect detection is important to avoid bias in studies evaluating mesocarnivore occupancy using remote camera traps (Lesmeister et al. 2015). We used single-season occupancy modeling to increase the number of sites, as We was not interested in immigration or emigration from sites among years.

We used stepwise model selection techniques (backward selection) to identify the factors influencing mesocarnivore detection probability and occupancy, where We started with a highly parameterized model and eliminated uninformative parameters based on their lack of influence on mesocarnivore detection probability or occupancy (Montgomery et al. 2012). Models related to mesocarnivore detection probability were fit prior to fitting models for local mesocarnivore occupancy. We pooled all mesocarnivore species for analyses due to low detection probabilities within each single species (MacKenzie et al. 2002). If a mesocarnivore was detected at a camera site during a sampling occasion, the site was considered occupied. Previous researchers have suggested, in grassland ecosystems with relatively high predator diversity, management actions to reduce grassland bird nest depredation may not prove successful if they do not consider the entire predator community (Renfrew and Ribic 2003, Pietz et al. 2012).

Prior to fitting occupancy models, we tested all covariates for multicollinearity, removing those which were highly correlated (Pearson's correlation estimate $|r| > 0.6$) from further analyses. Edge density at 100-m and 500-m spatial scales were correlated ($r = 0.66$), and edge density at 500-m and 1000-m scales were correlated ($r = 0.77$). We removed edge density at the 500-m spatial scale from further analyses because it was correlated across the other two spatial scales (100-m and 1,000-m), and this metric assessed at two scales was uncorrelated. Edge density (100-m) and distance to nearest wooded coulee were correlated ($r = -0.63$). We kept edge density and removed distance to the nearest coulee from analyses because mesocarnivores typically use habitat edges while hunting and foraging (Andrén 1995), and my metric of edge density includes wooded coulee, along with other habitat edges. For each variable included in detection and occupancy models, We evaluated whether a linear, quadratic, or pseudo-threshold (pseudo-asymptotic) effect (Franklin et al. 2000) was best supported for its influence on mesocarnivore detection probability or occupancy.

Variables included in the detection probability model were year, cattle presence, visit, Julian day (134–201), and the amount of precipitation during each 5-day visit. Variables included in the habitat model were cattle presence, edge density (100-m and 1,000-m spatial scales), and distance to nearest road or two-track, pasture fence, water feature, and oil pad. Once stepwise model selection was complete, we used Akaike's Information Criterion adjusted for finite samples (AIC_c) to evaluate model support and identify important variables to include in the final detection or abundance model. Supported models with large model weights (w_i) and AIC_c values ≤ 2 from the best-fit model were considered parsimonious (Burnham et al. 2011). When a supported model differed from the best-fit model by a single parameter, we considered the additional parameter to be uninformative and excluded this parameter from inclusion in the final model (Arnold 2010). We built a candidate model set for the management-scale effects on mesocarnivore occupancy based on *a priori* hypotheses, which included additive effects, along with 2- and 3-way interactions (Table 32). Factors hypothesized to affect mesocarnivore occupancy at the management-level were grazing system, stocking rate, and rangeland production potential.

Table 32. Candidate model set for the management-level effects on mesocarnivore occupancy in eastern Montana during 2016–17.

Model	**Description**
Null	Null Model
Mod1	Grazing System
Mod2	Stocking Rate
Mod3	Rangeland Production Potential
Mod4	Grazing System + Stocking Rate
Mod5	Grazing System + Rangeland Production Potential
Mod6	Stocking Rate + Rangeland Production Potential
Mod7	Grazing System + Stocking Rate + Rangeland Production Potential
Mod8	Grazing System × Stocking Rate
Mod9	Grazing System × Rangeland Production Potential
Mod10	Rangeland Production Potential × Stocking Rate
Mod11	Grazing System × Stocking Rate + Rangeland Production Potential
Mod12	Grazing System × Rangeland Production Potential + Stocking Rate
Mod13	Grazing System × Stocking Rate × Rangeland Production Potential

We assessed model fit for the best-fit model within habitat- and management-level analyses for mesocarnivores from 1,000 simulated datasets using the mb.gof.test function within AICcmodavg (Mazerolle 2013). Goodness-of-fit tests indicated $\hat{c}$ estimates between 1.3 and 1.5, and p-values < 0.1 for the most parsimonious models within each model set, providing evidence for potential overdispersion in the data. However, we identified the cause of lack-of-fit as two sites which had encounter histories of 11110, where the expected number of sites with this encounter history was 0.1, which substantially inflated the chi-square statistic. We temporarily removed these two sites with encounter histories 11110 from the analysis and re-ran the goodness-of-fit test, which resulted in $\hat{c}$ estimates between 0.7 and 1.0, and p-values > 0.95 for the most parsimonious models within each model set. These results indicated that the models adequately fit the data, and the original evidence for overdispersion was a result of two sites with unexpected encounter histories.

The best-fit model within habitat- and management-level analyses was used to generate predictions of mesocarnivore occupancy over the range of values for each variable, while holding other variables included in the best-fit model at their means. When multiple models shared support (ΔAIC_c values ≤ 2), model averaged estimates were used to generate predictions of mesocarnivore detection probability and occupancy.

Results

We recorded 178 mesocarnivore detections during 3,535 camera trap days at 164 remote camera sites located within 8 pastures managed for cattle grazing. We detected 5 species of mesocarnivores during camera trap surveys: American badger, coyote, raccoon, striped skunk, and weasel (*Mustela spp.*). Coyote was recorded at 69 of 164 camera sites, raccoon at 25 sites, American badger at 22 sites, striped skunk at 10 sites, and weasel at 4 sites. We recorded 4 species in pastures employing each of the three grazing systems: rest-rotation, summer-rotation, and season-long grazing systems. Striped skunk was not detected in season-long grazing systems, but weasel was only detected in season-long grazing systems.

Detection. – The average (± SE) probability of detecting a mesocarnivore at the study area was 0.298 ± 0.028. The top model describing mesocarnivore detection probability, with full support (AIC_c $w_i = 0.71$), included the main effects of year, cattle presence, visit, Julian day, and total precipitation (Table 33). Detection probability was higher in 2016 than 2017, higher when cattle were present at a site, and lowest during visit 5 compared to visits 1 – 4 (Table 34). The probability of detection increased with Julian day, and showed a quadratic relationship with precipitation, where detection was lowest when precipitation during the visit was moderate (15 – 25 cm; Table 34).

Table 33. Support for candidate models predicting observation-level effects on mesopredator detection probability and habitat-level effects on mesopredator occupancy in eastern Montana during 2016-17. Effects on detection probability include year, cattle presence, visit, Julian day, and precipitation. Effects on occupancy at the habitat-level include cattle presence, edge density (100-m and 1,000-m scales), and distance to the nearest road, fence, water, and oil pad. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i), and cumulative model weights (Cum w_i) are reported.

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_i**	**Cum w_i**
Detection					
Precipitation^2 + Date + Cattle + Year + Visit	11	734.48	0.00	0.71	0.71
Precipitation^2 + Date + Cattle + Year	7	737.74	3.26	0.14	0.85
Precipitation^2 + Date + Cattle	6	738.83	4.35	0.08	0.94
Precipitation^2 + Date	5	740.45	5.98	0.04	0.97
Precipitation^2	4	740.95	6.47	0.03	1.00
Null Model	2	754.55	20.08	0.00	1.00
Occupancy, habitat-level					
Edge Density (100-m) + Road + Fence + Water	15	713.35	0.00	0.28	0.28
Edge Density (100-m) + Road + Fence + Water + Edge Density (1,000-m)	16	713.39	0.05	0.28	0.56
Edge Density (100-m) + Road + Fence	14	713.62	0.27	0.25	0.81
Edge Density (100-m) + Road + Fence + Water + Edge Density (1,000-m) + Oil	17	714.93	1.58	0.13	0.94
Edge Density (100-m) + Road + Fence + Water + Edge Density (1,000-m) + Oil + Cattle	18	716.71	3.36	0.05	0.99
Null Model	11	734.48	21.13	0.00	1.00

[2] Variable indicates support for a quadratic effect.

ln(variable) indicates support for a pseudo-threshold effect.

Table 34. Standardized covariate estimates for the top mesocarnivore[a] models in eastern Montana during 2016–17.

	Estimates	
	β	SE
Detection probability		
Intercept	-0.76	0.30
Year, 2017	-0.46	0.25
Cattle presence, Yes	-0.49	0.25
Visit 2	-0.43	0.29
Visit 3	-0.25	0.31
Visit 4	0.26	0.31
Visit 5	-1.11	0.52
Julian day	0.22	0.14
Precipitation	-0.99	0.22
Precipitation^2	0.37	0.10
Occupancy, habitat		
Intercept	4.02	1.70
Edge density (100 m)	3.66	2.05
Distance to road	2.89	1.16
Distance to fence	-1.92	0.64
Distance to water	0.58	0.42
Occupancy, management		
Intercept	4.06	2.24

Season-long Grazing	-3.54	2.49
Summer-rotation Grazing	-3.44	2.10
Stocking Rate	1.64	1.10

[2] Variable indicates support for a quadratic effect.

[a] Mesocarnivore models include detections of American badger, coyote, raccoon, striped skunk, and weasel.

Habitat conditions. – After accounting for detection probability, four models shared support ($\Delta AIC_c \leq 2.0$) for habitat effects on mesocarnivore occupancy (Appendix H, Table H1). Models including the main effects of edge density (100-m), distance to the nearest fence, and distance to the nearest road had the majority of support ($w_i = 0.99$). The top habitat-level model describing occupancy of mesocarnivores included support for edge density (100-m), and distance to nearest road, fence, and water (Appendix H, Table H1). The probability of mesocarnivore occupancy increased with edge density (100-m; $\beta = 3.66 \pm 2.05$) and distance to nearest road ($\beta = 2.89 \pm 1.16$), and decreased sharply with distance to nearest fence ($\beta = -1.92 \pm 0.64$; Figure 17). Distance to nearest water was also included in the top model, but the 95% CI for effect size overlapped 0 and the effect was considered non-informative.

Management-level

Five models shared support ($\Delta AIC_c \leq 2.0$) for management-level effects on mesocarnivore occupancy (Appendix H, Table H2). Models including the main effects of grazing system, stocking rate, or rangeland production potential had the majority of support ($w_i = 0.67$). The top model included the main effects of grazing system and stocking rate ($w_i = 0.24$), the next top model included the main effect of rangeland production potential ($w_i = 0.13$), and the third supported model included the main effect of grazing system ($w_i = 0.11$). Mesocarnivore occupancy was highest in rest-rotation grazing systems, followed by season-long ($\beta = -3.54 \pm 2.49$) and summer-rotation systems ($\beta = -3.44 \pm 2.10$), and the probability of mesocarnivore occupancy increased with stocking rate ($\beta = 1.64 \pm 1.10$; Table 33, Figure 18).

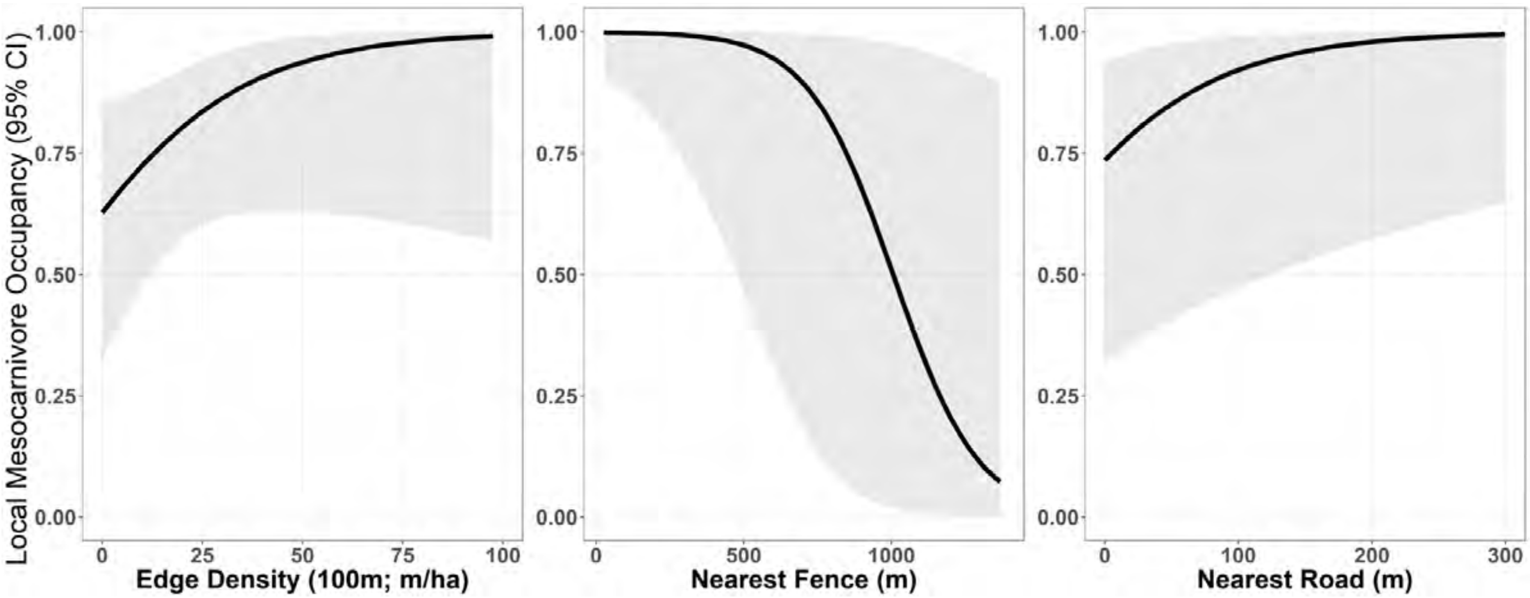

Figure 17. The top habitat model describing local occupancy of mesocarnivores in eastern Montana during 2016–17 included support for edge density (100-m), distance to nearest fence, and distance to nearest road. Distance to nearest water was also included in the top model, but the 95% CI for effect size overlapped 0 and the effect was considered non-informative.

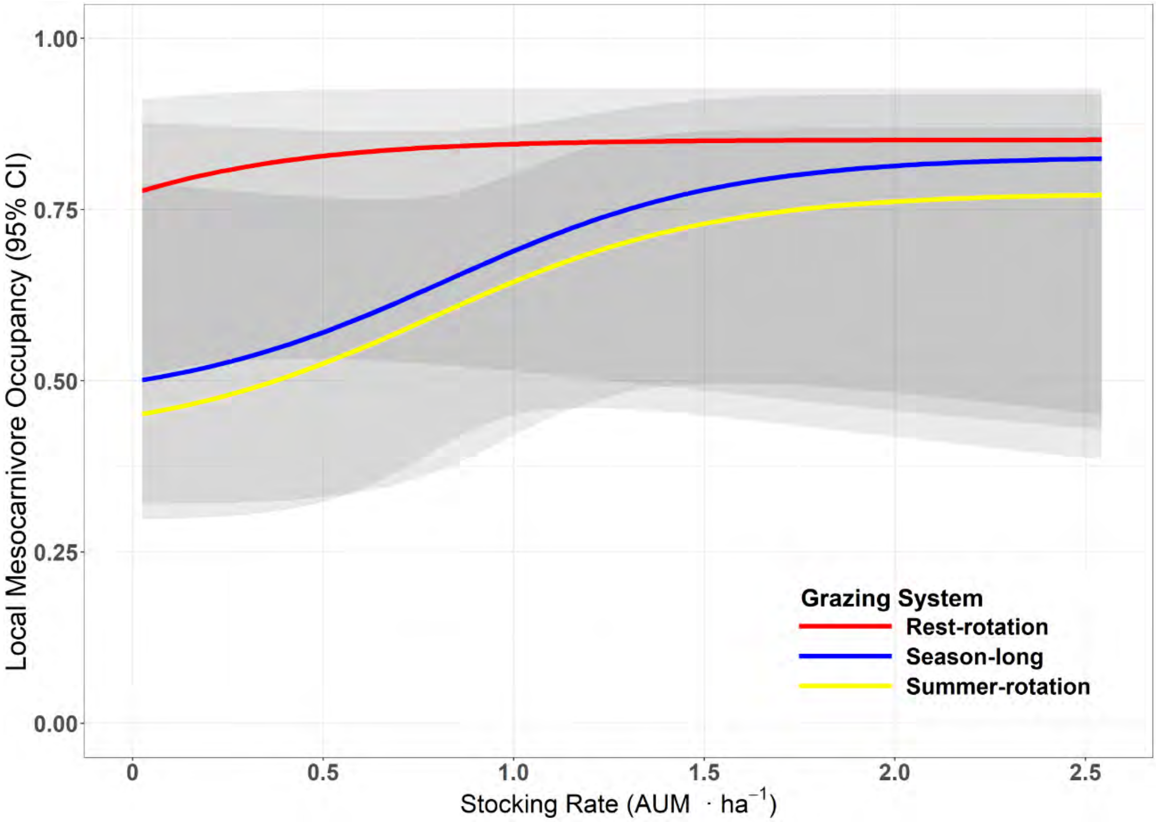

Figure 18. The top management-level model describing local occupancy of mesopredators in eastern Montana during 2016–17 included main effects of grazing system and stocking rate.

Published products from Objective 3

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.T. and L.B. McNew. 2018. Effects of livestock grazing management on occupancy of mesocarnivores in a northern mixed-grass prairie ecosystem. Montana State University College of Agriculture and Extension Research Report 4:40–44.

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Objective 4. Evaluate genetic diversity and pair-wise relatedness of female sharp-tailed grouse

Methods and Results

Loci and Genotyping. – Across 189 samples, we tested 24 microsatellite loci and one sexing locus (1237). Twelve loci were retained for complete genotyping of all samples (STGR_Primers_Cross.xlsx; top). Twelve loci were eliminated due to amplification and/or genotyping issues (STGR_Primers_Cross.xlsx; bottom).

Probability of Identity. – We quantified the power of our microsatellite locus panel to discern individuals using probability identity ($P_{(ID)}$; Evett and Weir 1998): the probability that two individuals drawn at random from the population could have the same genotype across all loci. We also calculated probability identity for siblings ($P_{(ID)sib}$): the probability that two siblings drawn at random from the population could have the same genotype across all loci. The 12 retained loci retained provided more than adequate cumulative power to discern amongst individuals and siblings ($P_{(ID)} = 3.61 \times 10^{-18}$; $P_{(ID)sib} = 1.77 \times 10^{-6}$).

Removal of Duplicate Samples. – Following genotyping, we identified and removed duplicate samples verified by genotyping (multiple captures of individuals 744, 1232, and 1331), resulting in 186 individuals genotyped. Individuals per lek ranged from 1 to 37 (median = 11, mean = 12.67 ± 11.91).

Genetic Diversity. – We calculated per-locus and per-lek average number of alleles (A), the effective number of alleles (Ae), the number of alleles with a frequency at least five percent (A95), the observed heterozygosity (H_O), the expected heterozygosity (H_E), and Wright's inbreeding statistic (F_{IS})—a measure of the departure from Hardy-Weinberg proportions—where $F_{IS} = 1 - (H_O/H_E)$ such that positive values indicate a deficit of heterozygotes while negative values indicate a excess of heterozygotes. Per-locus number of alleles ranged from 2 to 27 per locus (median = 13, mean = 14 ± 7.6), Ae from 2.0 to 17.6 (median = 6.8, mean = 7.6 ± 4.1), A95 from 2 to 9 (median = 6.0, mean = 6.2 ± 2.0), H_O from 0.47 to 0.93 (median = 0.83, mean = 0.78 ± 0.14), H_E from 0.50 to 0.94 (median = 0.85, mean = 0.83 ± 0.11), and F_{IS} from -0.04 to 0.43 (median = 0.036, mean = 0.059 ± 0.12). Per-lek number of alleles ranged from 1.8 to 11.7 per locus (median = 8.0, mean = 7.3 ± 3.2), Ae from 1.8 to 7.0 (median = 5.9, mean = 5.2 ± 1.7), A95 from 1.8 to 6.8 (median = 5.8, mean = 5.3 ± 1.5), H_O from 0.75 to 0.83 (median = 0.78, mean = 0.78 ± 0.03), H_E from 0.38 to 0.82 (median = 0.79, mean = 0.73± 0.13), and F_{IS} from -1.00 to 0.06 (median = 0.036, mean = 0.059± 0.12).

A, Ae, H_O, H_E, and therefore F_{IS}, were comparable to that which has been documented within greater sage-grouse across the northern tier of their range by Cross et al. (2016). Positive F_{IS} across all but two loci (BG16 & MS06.6) indicates a deficit of heterozygotes likely resulting from unaccounted for population substructure within the sample (i.e., the Wahlund effect) and from nonrandom mating within the sampled population. Highly positive F_{IS} at TUD3 may indicate the presence of a null alleles. Per-lek F_{IS} was largely centered around zero except for where few samples were collected.

We calculated individual-based genetic diversity including proportion of heterozygous loci in an individual (PHt), standardized heterozygosity based on the mean expected heterozygosity (Coltman et al. 1999), standardized heterozygosity based on the mean observed heterozygosity

(Hs_obs), internal relatedness (IR) (Amos et al. 2001), and homozygosity by locus (HL) (Aparicio 2006).

Genetic Divergence. – We calculated among-individual D_{PS} and analysis of molecular variance (AMOVA), and among-lek Bray-Curtis distance (a measure of genetic distance based upon the AMOVA distance metric found to perfectly correlate with D_{PS} by Shirk et al. 2017). Among-individual D_{PS} ranged from 0 to 0.96 (median = 0.25, mean = 0.26 ±0.08). Among-individual AMOVA ranged from 0 to 35 (median = 21, mean = 21± 3.6). Among-lek Bray-Curtis distance ranged from 0 to 0.05 (median = 0.04, mean = 0.03 ± 0.01).

Attached File Directory

See below for specifics of results included in the attached compressed directory "***STGR_GeneticResults.zip***"

Table: Per-locus genetic diversity across all samples (*by_locus_gendiv_stats.csv*).
Showing number of alleles (A), effective number of alleles (Ae), the number of alleles with at least 5% frequency (95%), observed heterozygosity (Ho), expected heterozygosity (He), Wright's inbreeding statistic ($F_{IS} = 1 - H_O/H_E$).

Table: Lek-based genetic diversity across all samples (*by_lek_gendiv_stats.csv*).
Showing number of alleles (A), effective number of alleles (Ae), the number of alleles with at least 5% frequency (95%), observed heterozygosity (Ho), expected heterozygosity (He), Wright's inbreeding statistic ($F_{IS} = 1 - H_O/H_E$).

Table: Individual-based genetic diversity (*by_indiv_gendiv.csv*)
Including (1) proportion of heterozygous loci (PHt) in an individual: PHt = number of heterozygous loci / number of genotyped loci, (2) standardized heterozygosity based on the mean expected heterozygosity (Hs_exp, Coltman et al. 1999): Hs_exp = PH_t / mean expected heterozygosity of typed loci, (3) standardized heterozygosity based on the mean observed heterozygosity (Hs_obs): Hs_obs = PHt / mean observed heterozygosity of typed loci, (4) internal relatedness (IR) (Amos et al. 2001): IR = $(2H–f_i)/(2N–f_i)$, where H is the number of loci that are homozygous, N is the number of loci and f_i is the frequency of the ith allele contained in the genotype, (5) homozygosity by locus (HL) (Aparicio 2006): HL = $E_h/(E_h+E_j)$, where E_h and E_j are the expected heterozygosities of the loci that an individual bears in homozygosis (h) and in heterozygosis (j), respectively.

Table: Proportion of shared alleles by individual (*by_indiv_dps.csv*)
Matrix format where rows and columns are individuals and values reflecting pairwise proportion of shared alleles are mirrored on either side of the diagonal.

Table: Analysis of molecular variance (*by_indiv_amova.csv*)
Matrix format where rows and columns are individuals and values reflecting pairwise differentiation are mirrored on either side of the diagonal.

Table: Bray-Curtis dissimilarity by lek (*by_lek_Bray.csv*)
Matrix format where rows and columns are leks and values reflecting pairwise differentiation are mirrored on either side of the diagonal.

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