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Sharp-tailed grouse occur across much of the northern Great Plains of North America where large grassland tracts remain. Though extirpated from areas within the Great Plains, primarily due to habitat loss, sharp-tailed grouse populations have remained relatively stable since European Settlement. Because of their need for large contiguous grasslands, sharp-tailed grouse typically occur in areas managed for or with cattle. In an effort to better understand how land management affects sharp-tailed grouse, we studied hen sharp-tailed grouse during the brooding season to identify habitat use and factors that influenced the daily survival rate of broods. We conducted our study on the Grand River National Grassland in South Dakota where cattle herbivory is the primary form of disturbance. We monitored 42 broods from 2013 to 2015. Using conditional logistic regression, we found brood-rearing hens used areas based on the distance to the nearest drainage and choose sites with less litter cover and bare ground relative to random sites at a microhabitat scale. Variables associated with variation in survival did not align with those shown to influence habitat selection. We found that brood survival decreased as the relative slope of a site increased and that survival increased as the distance a hen kept her chicks from a fence line also increased. At the microhabitat scale, survival was positively related to visual obstruction and vegetation height. Our findings demonstrate the importance of numerous variables across multiple scales to brood-rearing sharp-tailed grouse. Managers of grouse populations should manage for heterogeneity, as many factors appear to shape sharp-tailed grouse brood ecology in the Great Plains.

Keywords: grasslands, grouse, national grasslands, vegetation height, visual obstruction

Sharp-tailed grouse *Tympanuchus phasianellus* are a highly sought-after gamebird and native to much of North America's Great Plains. Of the three prairie grouse species that occur in the Great Plains (lesser prairie-chicken *Tympanuchus pallidicinctus*, greater prairie-chicken *Tympanuchus cupido*), sharp-tailed grouse historically have had the largest distribution with each of its six sub-species associated with different cover characteristics (Johnsgard 2002). Sharp-tailed grouse unlike prairie-chickens appear to show more plasticity in the cover they occupy. Sharp-tailed grouse occur in ecosystems dominated by grasslands, but also inhabit areas with a greater woody component (Johnsgard 2002). The population status for sharp-tailed grouse varies across their geographic distribution (Dyke et al. 2015, SD Game, Fish and Parks 2017). However, the loss of grasslands has resulted in a reduction in bird numbers and the eradication of sharp-

tailed grouse from certain regions (SD Game, Fish and Parks 2017).

Large expanses of relatively unfragmented grasslands provide the primary habitat for sharp-tailed grouse in the northern Great Plains (Johnsgard 2002). Persistent and on-going land use change and further fragmentation of grassland ecosystems have been catalysts responsible for the steady decline experienced by prairie grouse over the last half-century (Fischer and Lindenmayer 2007, Johnson et al. 2011, Fuhlendorf et al. 2017). Other factors related to declines in grouse may include overutilization of grassland cover by livestock (Sidle 2005), energy development (Hovick et al. 2014), and shifts in plant species composition. As global demand for energy, food and fibers increase, further land use changes should be anticipated generating the need for a greater understanding of grouse ecology in the northern Great Plains, which would allow managers to proactively mitigate negative impacts.

Sharp-tailed grouse often depend on landscapes that include grassland cover for many aspects of reproduction including brood rearing (Goddard et al. 2009, Johnson et al. 2011). The period of reproduction is of utmost importance

with respect to maintaining strong populations of grouse because of its influence on the number of birds recruited into the population each year (Peterson and Silvy 1996, Hagen et al. 2009, Milligan et al. 2018). While nesting certainly has its challenges for the hen, the time of brood rearing can also be difficult as hens lead precocial chicks in search of food and cover (Manzer and Hannon 2008). Brood-rearing hens must select areas that provide food for chicks, but also protect them from predators and the elements (Hagen et al. 2005). Previous studies have highlighted the influence of predation on juvenile grouse survival (Schroeder and Baydack 2001, Manzer and Hannon 2008). A brood-rearing hen should also select areas on the landscape that will help keep the brood warm or cool as young chicks have difficulty with thermal regulation (Ricklefs 1989, Marjoniemi et al. 1995, Pis 2002). Previous research has shown that cover characteristics (dense vegetation and bare ground) can influence the thermal environment surrounding sharp-tailed grouse nests (Raynor et al. 2018) and other research has demonstrated the differences in temperature that occur across a gradient of slopes and aspects, which may further influence how sharp-tailed grouse use the landscape (Suggitt et. al. 2011). The choices each hen makes regarding habitat selection and brood movement likely influence survival. Given the importance of brood survival for the maintenance of stable grouse populations (Peterson and Silvy 1996) and due to the current lack of information available to managers concerning sharp-tailed grouse brood ecology, research is needed that can provide a clearer understanding of how sharp-tailed grouse brood-rearing hens are using the landscape and how these selection choices may influence survival.

Because of their life history and association with large grassland landscapes, sharp-tailed grouse and other prairie grouse have been used by management agencies as indicator species (Roersma 2001). In particularly, the United States Forest Service (USFS) has used sharp-tailed grouse population trends to assess if their management actions were meeting goals and objectives (USFS 2001). While a target of national grassland management has been to maintain structure (vegetation height and density) following livestock herbivory for nesting hens (USFS 2001), little is known about the relationship that may or may not exist between brood-rearing hens and structure.

Throughout much of the sharp-tailed grouse's range, livestock production is an important economic land use. Livestock production can have both direct and indirect effects on local wildlife populations. Herbivory can manipulate the vegetation structure and thermal dynamics, which can affect breeding bird use of an area as structure has been found to be an important selection component for several grassland birds (Geaumont et al. 2017, Raynor et al. 2018). Beyond the direct effects of herbivory, the infrastructure (fences, water developments, roads, etc.) required to keep livestock can also influence bird use and survival (Fontaine et al. 2004, Wolfe et al. 2007, Stevens et al. 2012). Despite the importance of grasslands to sharp-tailed grouse and that livestock production is prevalent throughout their range, little information exists regarding the impact of infrastructure associated with livestock management on brood-rearing sharp-tailed grouse.

As economically valuable gamebirds and management indicator species, sharp-tailed grouse are heavily managed throughout their distribution, yet a general lack of information concerning the dynamics surrounding brood-rearing currently exists and may limit our ability to make accurate management decisions. With this in mind, we conducted research in which the main objectives were to evaluate habitat selection by brood-rearing hens and to assess brood survival in grasslands grazed by livestock to inform future management decisions concerning grouse in the Great Plains. In order to improve our knowledge of brood ecology, various landscape features and microhabitat characteristics were assessed including anthropogenic structures associated with livestock management. We predicted that brood-rearing hens would use sites nearer to grassland cover relative to other land uses and avoid areas that may be used more frequently by predators (fence lines and roads) in an attempt to improve brood survival (Christenson 1970, Prose 1987). Based on field observations from a previous study (unpubl.), we predicted that brood-rearing hens would select for drainage areas where vegetation stayed greener later in the summer when precipitation is generally scarce. We predicted hens would choose areas of flatter terrain (reduced slope) for brood-rearing as increased slope may influence air temperature, impair chick movement and allow predators to use the change in elevation to ambush unsuspecting chicks. We also predicted that aspect would influence hen selection of brood sites because of its influence on temperature (Suggitt et al. 2011). Furthermore, we expected that brood-rearing hens would select cover attributes that are important factors in maximizing brood survival.

Methods

Study site

Our study was conducted on the Grand River National Grassland (GRNG) in northwest South Dakota, USA (45°45′N, 102°30′W). The GRNG is 626 km² and managed for multiple uses by the USFS. The study area lies within the Missouri Plateau and is characterized as an upland plain. The topography is gently rolling to steep with several buttes present across the landscape. Private lands used for the production of livestock, crops and hay are intermingled within the GRNG. Mean annual precipitation is roughly 44 cm per year with the majority of the precipitation occurring from March through July (NOAA 2015). The area is characterized by cold winters and warm summers with mean annual temperatures of approximately 7°C.

The GRNG lies within the northern mixed-grass prairie and described by Barker and Whitman (1988) as a wheatgrass–needlegrass ecotype. Western wheatgrass *Pascopyrum smithii*, green needlegrass *Nassella viridula*, blue grama *Bouteloua gracilis* and little bluestem *Schizachyrium scoparium* are common graminoid species. Roughly 81 km² of the GRNG was used for crop production prior to the 1940s, at which time the land was reseeded to crested wheatgrass *Agropyron cristatum* – a drought tolerant non-native species. Heath aster *Symphyotrichum ericoides*, purple coneflower *Echinacea angustifolia*, western wall flower *Erysimum asperum* and

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non-native yellow sweetclover *Melilotus officinalus* are common forbs of the local plant community. Western snowberry *Symphoricarpos occidentalis*, skunkbrush sumac *Rhus trilobata*, buffalo berry *Sherpedia argentea* and silver sagebrush *Artemisia cana* are the primary species of upland woody vegetation on the GRNG.

Livestock production is an important industry in the region and much of the Grand River National Grassland is grazed by privately owned cattle (USFS 2001). The Grand River National Grassland is divided into allotments, which are further divided into pastures. Pastures are part of a larger 3–5 pasture deferred rotational grazing system; therefore, not all pastures are in use during the same period. Stocking rates among pastures ranged from 0.89 to 1.31 ha per animal unit month (AUM) and averaged 1.13 ha per AUM. Grazing dates varied from May to October. This is done as part of the USFS goal of long-term sustainability of livestock grazing that is listed as an objective in the Land Resource Management Plan for the GRNG (USFS 2001).

We captured hens on spring leks using walk in traps (Schroeder and Braun 1991). Annual selection of leks for trapping was made based on accessibility and number of attending males. Late spring snow and rain made certain leks inaccessible and these leks were not used. We trapped leks with at least four males as we found smaller leks more difficult to trap. If a lek was inaccessible one year, we considered it for trapping during future years if conditions allowed. Captured hens were fitted with a ~15 g necklace style VHF transmitters (Advanced Telemetry Systems, model no. A4120) an aluminum leg band, and then released on-site. We monitored collared birds 2–3 times per week using homing techniques to locate nests (White and Garrott 1990). Known locations were marked in hand-held global positioning systems. We avoided flushing birds until they were found on consecutive relocations in the same area. When a hen was located on consecutive monitoring events in the same area, we then flushed the bird from that location to determine if a nest was present. Once a nest was located, we used methods described by Westerskov (1950) to age eggs and estimate initiation date and approximate hatch date. We visually monitored nests 1–2 times per week to determine the fate of each nest, trying not to disturb hens during visits. We checked all nests on their expected hatch date to ensure an accurate assessment of nest fate and to get the best approximation of how many chicks hatched from a nest. If we were off on our expected hatch date, nests were visited every other day until fate was determined. Following hatch, hens with broods were monitored 2–3 times per week until 1 September. We used homing to get close (~10 m) to the hen without disturbing her and circled her location to obtain a used point. We flushed hens at least once per week to count chicks. If a brood was not easily detected (within 1–2 min of locating hen), little effort was made to verify brood occurrence, especially shortly after hatch to avoid stepping on chicks. As broods aged, more accurate counts were obtained by flushing hens and searching the immediate area for chicks.

Landscape variables of interest

We measured landscape characteristics of interest using map layers imported into ESRI ArcMAP (ver. 10.5). We paired each known brood location with two random points. We imported all known brood locations in a GIS layer and estimated a utilization distribution for each brood. We created a 288-m (average farthest daily movement) buffer around each utilization distribution and constrained random points to within the buffer (Hagen et al. 2005). If any buffer overlapped with a different brood's utilization distribution, we did not use random locations from within that portion of the buffer as another brood may have potentially used it (Hagen et al. 2005). We overlaid each known brood location and the random points onto a United States Department of Agriculture National Agriculture Imagery Program photo of the region taken in 2016. We used the aerial imagery to identify manmade objects (water tanks and windmills) within the grasslands. We obtained additional shape files from the Forest Service containing allotment boundaries, fences, underground pipelines and all roads within the grassland boundaries. The Forest Service classifies roads by management type (USFS 2005). In our analyses, we included roads belonging to categories two through five per USFS guidelines. A maintenance of level 5 indicated a paved, well maintained road. At the other end of the spectrum, a level 2 road is a 2-track where only high-clearance vehicles are recommended for travel. The majority of the level 2 roads are for access to water tanks and pumps for maintenance by the grazing association. We calculated the slope and aspect at each location from the United States Geological Survey (USGS) Digital Elevation Model (DEM) with 10 m resolution as both factors might influence habitat use by grouse (Norton et al. 2010, Dzialak et al. 2011). Finally, we used the USGS National Hydrology Dataset to identify drainages throughout the grasslands. Drainages not only included rivers and streams, but more frequently included low areas were water drained from the surrounding topography during snow melt and rain events. With the Near function in Analysis Tools of the ArcToolbox, we calculated the distance from each brood and random location to the nearest water tank, road, road by management category, fence and to the center of the nearest drainage.

Habitat use and survival for many game birds is influenced by land use and cover types (Matthews et al. 2011, Geaumont et al. 2017). Sharp-tailed grouse prefer areas dominated by grasslands and it may be expected that the presence of other land use and cover types in the surrounding area may influence selection of brood rearing habitat as well as influence brood survival. We identified land use at each brood and random location and calculated the distances from each point to the other land use types using the 2011 National Land Cover Database raster layer from the Multi-Resolution Land Characteristics Consortium (USGS 2014). Within the land cover layer, all development intensities, forest classifications, grassland classifications and wetland classifications were simplified into a single classification for their respective cover type. We also calculated an edge measurement by calculating the distance to the nearest change in land use.

Microhabitat variables of interest

Microhabitat variables of interest were assessed at every third location for each hen known to have a brood. Vegetation was evaluated along two perpendicular 12 m transects. One transect ran east–west, while the other north–south. A 1-m^2

frame was used to visually estimate the percent canopy cover of grasses, forbs, litter and the amount of bare ground at 2-m intervals along each transect for a total of 12 readings per brood location. We classified litter as all dead standing vegetation within the canopy (Geaumont et al. 2017). Our estimate of bare ground included all mineral soil observed through the canopy. Two field specialists completed all canopy cover estimates to provide consistency among years. We quantified visual obstruction and maximum vegetation heights using a modified Robel Pole at 2-m intervals (Robel et al. 1970, Benkobi et al. 2000). The pole was observed from a distance of 4 m and a height of 1 m from the four cardinal directions. We recorded the first demarcation not completely obstructed by vegetation. We measured similar vegetation characteristics at one random site per brood location on the same day vegetation was measured at the brood location. Random locations were kept within 100-m of the used location and within the same allotment. We choose to keep random locations within 100-m of a used location because we believed based on previous years observations that this was roughly the average distance a hen moved her brood during a 24 h period. We also choose to keep random locations within the same allotment during microhabitat assessment as to not sample across different management schemes (i.e. grazed versus not grazed) that would influence vegetation characteristics differently and may influence use. We were interested in learning what it was about vegetation differences that lead brood-rearing hens to select one area over another within a certain allotment.

Statistical methods

Brood habitat selection
We used conditional logistic regression to assess the odds of sharp-tailed grouse hens selecting brood sites based on used and available resources at two different scales (Hosmer and Lemeshow 2000, Goddard et al. 2009). We considered brood locations independent data points as the used locations were conditioned against the random locations in the conditional logistic regression (Dixon 2008). We evaluated a random effects structure using a random intercept for each hen, but did not find it to be informative, so instead use a fixed effects structure during analyses (Duchesne et al. 2010).

We created two separate model sets to evaluate the effect of habitat variables of interest on brood-rearing habitat selection. First, we constructed a group of 18 a priori models based on landscape level habitat variables of interest that were measured using GIS and based on biological reasoning and past research (Atamian et al. 2010, Norton et al. 2010, Matthews et al. 2011). We grouped landscape variables by natural and manmade features. We tested both linear and quadratic forms of the covariate groups (Hamerstrom et al. 1957, Buhnerkempe et al. 1984, Matthews et al. 2013, Geaumont et al. 2017). Models that included the quadratic form of a variable also included the linear form. Prior to modelling procedures, we assessed multicollinearity among variables using a Pearson correlation coefficient of $|r| \geq 0.6$. Only aspect and distance to nearest shrub cover were correlated ($r = 0.71$). These variables were not included in the same models. Next, a set of 15 a priori microhabitat vegetative models were constructed.

We tested both linear and quadratic forms of all variables of interest. Pearson's correlation revealed no correlated microhabitat variables at the $|r| \geq 0.6$ level.

Models from each scale were ranked using Akaike's information criterion corrected for small sample size (AICc) and Akaike weights were used as evidence of support for each model (Burnham and Anderson 2002). We considered all models with a $\Delta AICc \leq 2$ of the top model to be valuable (Burnham and Anderson 2002). We constructed odds ratios for all variables included in the top model set whose 95% CI of the coefficient estimate did not include zero (Anteau et al. 2012). We used the survival package in R to develop the conditional logistic regression models (Therneau 2015).

Brood survival
The nest survival model in Program Mark was used to assess the effect of landscape and microhabitat variables on the daily survival rates of sharp-tailed grouse broods (White and Burnham 1999). We used the nest survival model opposed to other known fate options due to the unequal relocation intervals of broods during our study (White and Burnham 1999). We used the same model sets during the analysis of survival as were evaluated during the analysis of brood habitat use. In addition to evaluating the effect of habitat variables on brood survival, we first developed a model set to assess the effect of temporal variables on brood survival. We compared a constant survival model to models that included year, time trends to evaluate if brood survival varied during different periods in the season, and age to identify if survival increased as the brood aged (Goddard and Dawson 2009). Changes in predator populations and seasonal shifts in weather patterns may influence survival (Flanders-Wanner et al. 2004). We averaged individual habitat variables of interest across all brood locations for each hen and used these values as covariates in the survival models (Hagen et al. 2005). We included a constant survival model that contained no covariates in each model set for comparison.

Models from each set were ranked using AICc and Akaike weights were used as evidence of support for each model (Burnham and Anderson 2002). We considered all models with a $\Delta AICc \leq 2$ of the top model to be valuable (Burnham and Anderson 2002). We considered covariates within supported models whose 95% CI of the coefficient estimate included zero as having no influence on survival. We standardized days within the brooding season with 1 June being the earliest day we encountered a brood and 1 September being the last day broods were monitored. Our standardized brooding season resulted in 93 estimates of daily survival. Our survival estimate interval spans a greater period of time than previous studies, but based on experience we were comfortable differentiating adult from juveniles until 1 September (Manzer and Hannon 2008, Goddard and Dawson 2009). Beyond 1 September we found an increased number of hens without broods or with noticeably fewer birds than previously recorded and it was likely around this time that brood dispersal occurred (Norton 2005). We considered a brood successful if at least one chick survived the monitoring period. We reported survival across a 60-day period and use the Delta Method to estimate variance (Seber 1982). We used a logit link function during survival modeling procedures.

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Results

Brood habitat use

We collared 28, 15 and 42 hens from 2013 to 2015, respectively. We used data collected from 14 broods in 2013, 9 broods in 2014 and 18 broods in 2015. Hens with broods were captured at 17 different leks. Hens with broods had average daily movement distances of 96 m (SE = 6.36) across all years of study. Monitoring efforts resulted in 427 known brood locations with microhabitat characteristics evaluated at 149 of them (Table 1). The number of points per brood included in the analyses ranged from 1 to 10 with those broods that survived longer contributing more data. Of the 427 known brood locations, 92% occurred in grasslands, 4% in cropland, 1% in hay land and the remaining 3% occurred in developed areas, primarily farmsteads.

We found brood-rearing hens selected resources at the landscape level based on distance to the nearest drainage as our top model contained the linear and quadratic version of the variable (Table 2). Brood-rearing hens typically selected areas nearer to a drainage center and as the distance to the nearest drainage increased the odds of use declined ($\beta = -0.006$, SE = 0.001, CI = -0.008 to -0.003) with some leveling off at distances beyond 700 m ($\beta = 6.02 \times 10^{-6}$, SE = 3.00×10^{-6}, CI = 1.50×10^{-7} to 1.19×10^{-5}; Fig. 1). The model that included only the linear version of distance to drainage also received support and was 1.8 AICc points different from our top model (Table 2). Additional models were not supported as indicated by ΔAICc values >2.

Table 1. Average (mean) and standard error for landscape and microhabitat variables of brood rearing hen sharp-tailed grouse of the Grand River National Grassland from 20013 to 2015 in northwestern South Dakota.

Variable	Brood location Mean	Brood location SE	Random point Mean	Random point SE
Landscape variables				
Distance to fence (m)	368	14	406	10
Distance to wind/water (m)	951	33	784	15
Distance to road (m)	336	14	349	11
Distance to wetland (m)	1509	33	1424	25
Distance to forest (m)	2273	48	2205	35
Distance to development (m)	351	15	344	11
Distance to water (m)	1347	31	1317	24
Distance to grassland (m)	6	4	8	1
Distance to shrubs (m)	2088	53	2058	37
Distance to pasture/hay (m)	1386	42	1332	30
Distance to crops (m)	1021	35	1033	26
Distance to drainage (m)	128	6	167	4
Distance to land use change (m)	239	12	225	7
Aspect (degrees)	171	5	176	3
Slope (rise/run (m))	4	0.1	3	0.1
Microhabitat variables				
VOR (cm)	11.7	0.7	9.3	0.6
Litter depth (cm)	1.1	0.1	1.0	0.1
Maximum height (cm)	61.4	1.7	55.8	1.8
% grass	45.4	1.6	44.6	1.5
% forb	19.4	1.4	14.9	1.2
% shrub	1.4	0.4	0	0.2
% sedge	5.0	0.9	5.8	0.8
% bare ground	5.1	0.3	6.8	0.5
% litter	23.6	1.3	27.7	1.4

The top microhabitat model indicated the odds of a brood-rearing hen using a site increased when both litter cover ($\beta = -0.04$, SE = 0.01, CI = -0.08 to -0.008) and bare ground decreased ($\beta = -0.15$, SE = -0.04, CI = -0.24 to -0.06; Fig. 1). The top model also included canopy cover of grasses ($\beta = -0.01$, SE = 0.01, CI = -0.04 to 0.02) and forbs ($\beta = 0.02$, SE = 0.02, CI = -0.01 to 0.06), but the CI for each coefficient estimate included zero indicating no impact on brood use (Table 2). All other models were not competitive as indicated by ΔAICc values >2.

Brood survival

Ten of forty-one broods monitored during our study failed, of which six did so before 25 days post-hatch and the remaining four failed by 41 days post-hatch. Successful broods were monitored for an average of 77 ± 2.5 days (hatch to 1 September) with the monitoring period ranging from 45 to 93 days. Eighty-four percent of successful broods were monitored for longer than 60 days. The constant daily survival model was the top temporal model evaluated (Table 2). While other temporal models received support, the 95% CI of the coefficient estimates from each model included zero, indicating no impact on survival. The DSR of broods based on our constant daily survival model was 0.997, SE = 0.001 which resulted in a brood survival of 0.84 ± 0.05 across a 60-day period. Variation in daily survival rates for sharp-tailed grouse broods at the landscape level was a function of slope, aspect and distance to nearest fence (Table 2). The top model was 3.7 AICc points better than the second-best model and indicated that brood survival decreased as the average slope of the land increased ($\beta = -0.70$, SE = -0.33, CI = -1.4 to -0.05; Fig. 2). The top model further suggested that survival decreased as the average distance a hen kept her brood from a fence also decreased ($\beta = -0.006$, SE = 0.003, CI = 0.0005–0.01; Fig. 2). Though included in the top model, the 95% CI of the coefficient for aspect included zero indicating no effect on survival ($\beta = 0.01$, SE = 0.01, CI = -0.006 to 0.04).

At the microhabitat scale, brood survival was a function of quadratic VOR and linear maximum vegetation heights (Table 2). Based on the top model, the daily survival rate of broods increased as VOR increased above 2.54 cm and declined as VOR reached levels above 25.4 cm (linear VOR, $\beta = 1.9$, SE = 0.5, CI = 1.0–2.8; quadratic VOR; $\beta = -0.19$, SE = 0.05, CI = -2.8 to -0.09; Fig. 2). Daily survival rates also increased as maximum vegetation heights increased ($\beta = 0.25$, SE = 0.1, CI = 0.05–0.44; Fig. 2). The second-best model was 2.0 ΔAICc from the top model and included the addition of quadratic maximum vegetation height; however, the 95% CI of the coefficient estimate included zero indicating no impact on survival ($\beta = 0.001$, SE = 0.02, CI = -0.03 to 0.4; Table 2).

Discussion

National Grasslands across the Great Plains of North America provide a stronghold for many remaining prairie grouse populations. In our study of sharp-tailed grouse brood habitat use and survival, we found several factors across scales

Table 2. Models with Δ AICc scores ≤ 2 for selection and survival models of brood rearing hen sharp-tailed grouse on the Grand River National Grassland from 2013 to 2015 in northwestern South Dakota. % grass, % forbs, % litter, and % bare ground represent the percent canopy cover of each variable surrounding brood locations.

	K	Δ AICc	ω_i	Cum. ω_i
Landscape selection				
Dist to drainage + Dist to drainage²	2	0.0	0.71	0.71
Dist to drainage	1	1.8	0.29	1.00
Microhabitat selection				
% grass + % forbs + % litter + % bare ground	4	0.0	0.86	0.86
Temporal survival				
Constant	1	0.0	0.33	0.33
Time	2	0.64	0.24	0.57
Time + Time²	3	1.36	0.17	0.74
Age	2	1.75	0.14	0.88
Landscape survival				
Slope + Aspect + Dist to fence	4	0.0	0.63	0.63
Slope + Aspect	3	3.7	0.10	0.73
Dist to fence + Dist to water + Dist to development + Distance to nearest road	5	4.0	0.09	0.82
Microhabitat survival				
VOR + VOR² + MxHt	4	0.0	0.55	0.55
VOR + VOR² + MxHt + MxHt²	5	2.0	0.20	0.75
VOR + VOR² + MxHt + % bare ground + % bare ground²	6	3.3	0.11	0.86

influenced brood ecology on the GRNG. At the landscape scale, habitat selection of brood-rearing hens was positively associated with drainages while at a microhabitat scale brood-rearing hens used areas with less bare ground and litter cover relative to random locations. Factors important to use were not the same factors found to be important to brood survival. Both increased slope and decreased distance to fence affected survival at the landscape level while VOR and vegetation height were important factors related to survival at the microhabitat level. While factors varied between use and

survival, our findings show management can influence the majority of variables important to brood-rearing hens.

Our findings concerning the positive association between drainages and brood-rearing hens confirmed our hypotheses from a previous pilot study. On the GRNG, we observed vegetation in these areas remained greener longer into the summer when other vegetation within the landscape had senesced. Why brood-rearing hens were attracted to these areas is unclear, but we offer two potential explanation for these findings. First, Acrididae, the family in which grasshoppers
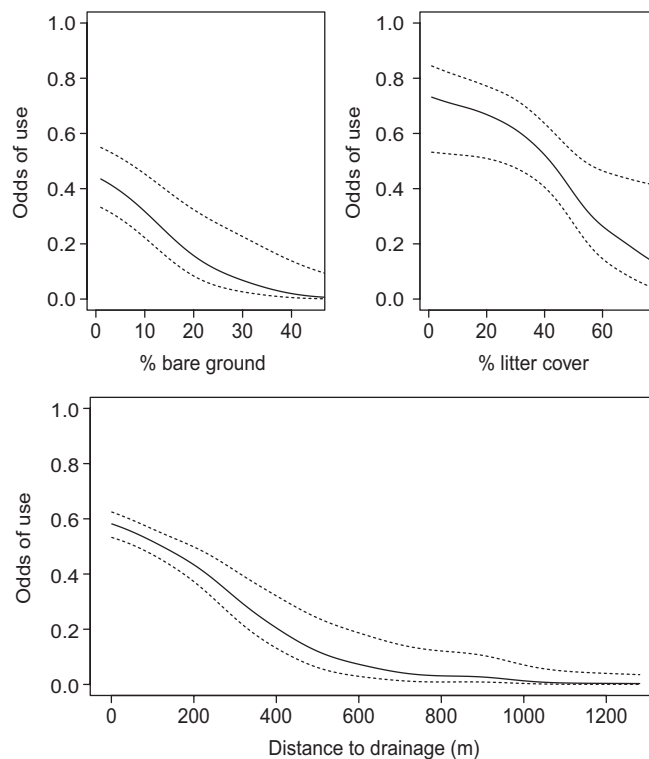

Figure 1. Odds of use by brood rearing sharp-tailed grouse for covariates from the top conditional logistic regression of the landscape and microhabitat models for broods in the Grand River National Grassland, South Dakota, 2013–2015. Variables not plotted were held constant at their means. Dashed lines represent a 95% confidence interval.
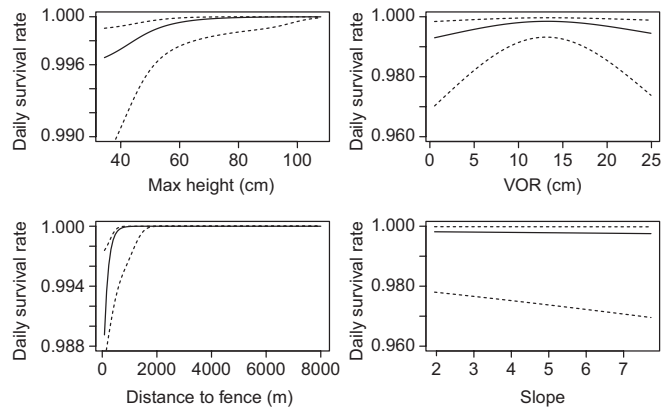
Figure 2. Daily survival rates of brood rearing sharp-tailed grouse in the Grand River National Grassland, South Dakota, 2013–2015, based on the top landscape and microhabitat models produced using Program MARK. Variables not plotted were held constant at their means. Dashed lines represent a 95% confidence interval.

belong, are important food sources for prairie grouse especially during brood rearing (Hagen et al. 2005, Sullins et al. 2018). Previous studies have found grasses to be important forages for grasshoppers and further reported grasshoppers moving into lower areas of greener vegetation (Dempster 1963, Lambley et al. 1972). Perhaps brood-rearing hens were following grasshoppers and other members of the Acrididae family into these greener drainage areas. A second explanation may be related to the thermal environment provided to grouse in these areas. Recent work has demonstrated the importance of thermal refugia for nesting birds (Hovick et al. 2014, Tanner et al. 2017, Raynor et al. 2018) while others have demonstrated the role of the thermal environment on the survival of chicks (Ruthrauff and McCaffery 2005, Kochert et al. 2019). Given the importance of these areas to brood-rearing hens, future work is needed to better understand the relationship we observed during our study.

Though our study demonstrates the importance of drainages for brooding grouse, other fine scale factors played a role in how brood-rearing hens used an area. At the allotment level, brood-rearing hens tended to use areas with less bare ground than occurred at random sites as areas with ≥40% bare ground were seldom used (Fig. 1). As the proportion of bare ground increased it is plausible that there was not enough vertical cover to adequately protect chicks from weather extremes or to provide camouflage from predators, as thermal regulation and concealment from predators are key to chick survival (Hannon and Martin 2006, Carroll et al. 2015). Previous studies regarding prairie grouse detail mixed findings with respect to brood-rearing hens and bare ground. Brood-rearing sharp-tailed grouse on the Fort Pierre National Grassland in central South Dakota demonstrated avoidance of areas with greater bare ground relative to random locations while greater prairie-chickens with broods were not affected by changes in bare ground (Norton et al. 2010). Matthews et al. (2011) reported greater prairie-chickens selected brooding cover with increased bare ground relative to random points; but also found brood-rearing hens preferred conservation reserve program (CRP) grasslands where disturbance was minimal compared to other grassland cover where disturbances, such as grazing and burning, were more prevalent. Findings from the Sandhills region of Nebraska concerning greater prairie-chicken

brood-site selection align with our findings as brood-rearing hens typically selected sites with less bare ground relative to random locations (Anderson et al. 2015).

In addition to bare ground, the percentage of standing dead litter cover in the canopy also influenced how brood-rearing hens used the landscape as hens tended to avoid areas with greater litter cover relative to random sites (Fig. 1). Our findings here are unique, as other studies have reported no effect of standing litter on brooding prairie grouse (Goddard et al. 2009, Hagen et al. 2013, Anderson et al. 2015). While we found no influence of canopy composition on use, the accumulation of standing dead litter can influence the surrounding plant community and may have resulted in conditions unfavorable to brooding hens (Facelli and Pickett 1991). Standing litter intercepts light and can restrict seedlings of beneficial plants, such as forbs, from establishing. Litter may influence the thermal environment (Raynor et al. 2018), which may influence the ability of brood-rearing hens to keep chicks at optimal temperatures especially during the first few days following hatch when chicks are less able to thermoregulate (Hannon and Martin 2006). Finally, excessive standing litter may also restrict the ability of young chicks to navigate through grassland cover (Matthews et al. 2011).

The 84%, 60-day brood survival estimate we report during our study is among the greatest reported for sharp-tailed grouse. Only the Fort Pierre National Grassland in central South Dakota report greater survival with broods experiencing an 89% survival rate (Norton 2005). Similar to our study, Norton (2005) monitored broods until late August. In British Columbia, sharp-tailed grouse brood survival was 67% across the 35-day monitoring period (Goddard and Dawson 2009). The first 35-days following hatch are known to be a dangerous time for young grouse and supported by our observations (Goddard and Dawson 2009, Schole et al. 2011, Anderson et al. 2015). Based on our DSR of 0.997, our 35-day survival for monitored broods was near 90%. Unlike studies previously referenced, others have not used a method to account for biases in survival data and instead reported apparent brood survival rates across various monitoring intervals for sharp-tailed grouse including 37% in Wisconsin (Connolly 2001; monitored hatch to mid-August), 32% in Alberta (Roersma 2001; monitored hatch to early-August)

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and 47% in central Montana (Bouaquet and Rotella 1998; monitored 56 days post-hatch). Broods during our study had a 60-day post-hatch apparent brood survival rate of 74%. However, we caution readers about the reliability of comparisons of apparent brood success across studies because as pointed out by Bouaquet and Rotella (1998), these estimates can be biased making them incomparable.

Our findings concerning factors important to brood survival did not directly align with those found to be important during cover selection. This leads us to reject our prediction that habitat features considered important during selection would also be attributes that maximize brood survival. The potential disconnect we observed between selection and survival may have long-term implication for grouse populations on the GRNG as hens used areas that may reduce chick survival. For example, brood-rearing hens that are avoiding areas with greater litter cover may inadvertently lead chicks into areas that do not provide the necessary VOR or vegetation height needed to conceal chicks from predators and thus leading to increased predation rates and decreased survival.

Alternative factors to those important during selection at both the landscape and microhabitat level influenced the survival of broods on the GRNG. Sharp-tailed grouse brood survival increased as the distance to the nearest fence increased (Fig. 2). Results concerning the impact of fences on prairie grouse survival have been mixed and may be related to the amount of fence in an area (Robinson et al. 2016). For instance, the risk of fence collisions by lesser prairie-chickens in Kansas and Colorado was limited and reported to have little biological significance to these populations (Robinson et al. 2016). Conversely, others have previously reported the negative impact of fence lines on sage-grouse (Stevens et al. 2012), greater prairie-chickens (Toepfer 1988) and lesser prairie-chickens in Oklahoma and New Mexico (Wolfe et al. 2007), primarily related to collisions, but few other studies concerning sharp-tailed grouse brood survival have evaluated these effects. Though not observed during our study, fence collisions may result in grouse fatalities, especially for young chicks learning to fly, however, we speculate that it is more likely that the relationship that exists between predators and fence lines influenced our findings concerning survival. Fence lines can provide travel corridors for mesopredators and perches for aerial predators, both of which commonly prey on grouse (Pedlar et al. 1997, Hannon and Martin 2006). The primary management tool used on the GRNG is livestock production and due to the current deferred rotational grazing systems in place, hundreds of km of barbed wire fence are stretched out across the landscape.

Though the overall effect was minimal relative to other factors of importance (Fig. 2), we found brood-rearing hens that used areas of lesser slope experienced greater brood survival compared with hens that more frequently used areas of steeper grades. There are at least two potential reasons for this finding. First, at the study site, upland areas with greater slope generally have less productive soils and consist of a different plant community relative to level landscapes, which could lead to less concealment cover for chicks (Nippert et al. 2011, Soil Survey Staff 2018). Second, is that increased slope may make it easier for a predator to approach unsuspecting chicks and restrict a young grouse's ability to disperse during a predator attack (Whittingham et al. 2002).

The idea that slope can affect sharp-tailed grouse brood survival has not been thoroughly assessed elsewhere, but should be considered further as other grassland birds have also been found to use flatter terrain during the breeding season (Manzer and Hannon 2008, Goddard and Dawson 2009, Gennet et al. 2017).

Visual obstruction and maximum vegetation height were key microhabitat components resulting in greater survival of sharp-tailed grouse broods. Visual obstruction and plant height are both important structural components when it comes to a hen's ability to conceal herself and her chicks from predators (Anderson et al. 2015, Schreiber et al. 2015). Brood-rearing hens across the GRNG experienced greater brood survival when VOR ranged from 5 cm to 20 cm, but declined at VOR beyond 20 cm. Perhaps in areas where VOR exceeds 20 cm the vegetation begins to affect the thermal environment near the ground surface. This causes the area to maintain greater moisture and potentially leads to greater cooling which could have a negative effect on chicks during the early stages of brood rearing. An alternative explanation may be that it is more difficult for broods to see approaching predators in the dense vegetation. Previous studies regarding sharp-tailed grouse have not reported nor often evaluated a direct link between VOR or vegetation height and brood survival (Manzer and Hannon 2008, Goddard and Dawson 2009). Others have assessed the impact of VOR on the survival of greater and lesser prairie-chicken broods, but often report no effect on survival (Fields et al. 2006, Matthews et al. 2011, Anderson et al. 2015).

Conclusions

We acknowledge that our landscape level results may have been different had we selected a different scale or area at which to access use and survival. However, at an area slightly larger than the utilization distribution of brood-rearing hens, between hatch and dispersal, our results further exemplify how wildlife frequently make habitat use decisions across scales and these decisions are not always directly related to survival. Management of the GRNG is typical of National Grassland management across the Great Plains where cattle herbivory is a management tool frequently used. Our findings demonstrate that grouse brood ecology is impacted by variables managers cannot manage such as slope, but also influenced by factors that can be managed including the percent bare ground, standing litter cover and VOR as well as the miles of fence used to manage livestock movement. Our data show that heterogeneity of grassland characteristics will benefit grouse given the variety of variables important to brooding hens. Finally, given that fences negatively impacted brood survival, we suggest that research is needed to evaluate other grazing practices in sharp-tailed grouse habitats that can affect livestock distribution through other means then fencing (e.g. patch-burn grazing).

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commitment to the National Grasslands and grouse is unmatched. Your willingness to share that enthusiasm and knowledge greatly improved our research.

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