

EFFECTS OF GRAZING MANAGEMENT ON SHARP-TAILED GROUSE ECOLOGY IN
MIXED-GRASS PRAIRIES

by

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ABSTRACT

Many grassland species co-evolved with large herbivores and require habitats along the entire structural gradient created by grazing. Widespread declines of grassland birds, however, have prompted concerns about rangeland management. Conceptually, rest-rotation grazing functions as a conservation strategy to mimic historic disturbance regimes and create pasture-level heterogeneity in the absence of fire, but its utility for improving grouse habitat has not been tested. We evaluated rest-rotation grazing as a conservation management technique compared to traditional grazing systems, including summer rotation and season-long grazing, and assessed the effects on sharp-tailed grouse (*Tympanuchus phasianellus*), an indicator species for grassland ecosystems. We monitored radio-marked female sharp-tailed grouse in eastern Montana and western North Dakota during 2016–2018 to monitor nesting ecology, adult survival, and habitat selection. Both nest site selection and nest survival were directly related to vertical nesting cover, which was only weakly related to grazing management variables, including grazing system and stocking rate, at moderate stocking rates (≤ 2 AUM ha⁻¹). Cattle presence during the nesting period had a positive effect on daily nest survival, potentially because either the cow or rancher presence affected predator behavior. Grazing management did not have a meaningful influence on any aspect of the overall survival of adult female sharp-tailed grouse, although seasonal patterns of mortality risk differed among systems. More importantly, cropland increased mortality risk of adult female sharp-tailed grouse. At broad spatial scales, females selected for grassland habitats, but exhibited limited to no selection for either landscape or management variables when selecting habitat at smaller spatial scales. We found limited evidence that grazing management was a driver of habitat selection at either spatial scale examined. Furthermore, female sharp-tailed grouse exhibited strong individual variation in both home range size and third-order habitat selection. Taken together, our results suggest that rest-rotation grazing did not influence any aspect of sharp-tailed grouse ecology we studied relative to other grazing systems and did not increase pasture-level heterogeneity in relevant vegetation variables. Therefore, grazing management strategies with moderate stocking rates that preserve large intact grasslands are a better conservation strategy for sharp-tailed grouse than prescribing specific grazing systems.

INTRODUCTION AND LITERATURE REVIEW

Grasslands are a globally important ecosystem, covering an estimated 25-40% of the terrestrial planet and providing critical habitat for a variety of plants and animals (White et al. 2000, Boval and Dixon 2012, Blair et al. 2014). Economic benefits of grasslands notably include livestock production, but grasslands also provide crucial ecosystem services that are often undervalued, including climate regulation, soil conservation, and the provisioning of genetic resources. A combination of high belowground biomass and relatively slow decomposition rates produces an accumulation of organic matter and nutrients in grassland soils (Blair et al. 2014). As a result, grasslands play a major role in global biogeochemical cycles, sequestering large amounts of carbon and other nutrients that are rapidly transferred to the atmosphere when land is converted to cropland (Sala and Paruelo 1997, Blair et al. 2014). In addition, the large root systems of grasslands conserve soil by preventing erosion (Sala and Paruelo 1997). Finally, as the majority of domesticated animals and crops originated there, grasslands represent an important source of genetic resources that have a disproportionately large conservation value (Sala and Paruelo 1997).

Despite their array of benefits, temperate grasslands are one of the ecosystems most altered by human activity and suffering from the greatest levels of habitat loss and degradation (Hoekstra et al. 2005, MEA 2005). Recent estimates suggest that the majority of grasslands have been degraded enough to have lost some degree of carrying capacity (Blair et al. 2014). Grasslands are primarily under stress due to land conversion to cropland and excessive grazing pressure (Alkemade et al. 2013, Blair et al. 2014).

However, additional threats include climate change, habitat fragmentation, exurban development, changes in natural disturbance regimes, and shrub encroachment (Askins et al. 2007, Alkemade et al. 2013, Blair et al. 2014). Mixed grass prairies, in particular, have lost most of their original land, with only an estimated 25% of historic prairie intact in states like North Dakota and Nebraska (Johnson and Bouzaher 1995, Askins et al. 2007). The loss and degradation of grasslands can have cascading negative effects, including the extinction and decline of many populations and species, changes in ecosystem function, and the deterioration of ecosystem services (Ceballos et al. 2010). Grassland birds are an excellent example, having experienced more significant and widespread declines in the past decades than any other guild of birds in North America (Knopf 1994). For example, 22 of 25 obligate grassland species in mixed grass prairies are declining (Sauer et al. 2013).

Upland game birds have often been used as an indicator for grassland conservation, because identifying sustainable management for game birds can benefit a suite of associated species (Poiani et al. 2001, Roersma 2001, Brennan and Kuvlesky Jr. 2005, Donnelly et al. 2017). Sharp-tailed grouse (*Tympanuchus phasianellus*) are the most adaptable and widely distributed of all prairie grouse (*Tympanuchus* spp.), historically occurring in 21 states and 8 Canadian provinces (Schroeder 2004). There are six extant subspecies of sharp-tailed grouse, two of which were native to Montana: the Columbian sharp-tailed grouse (*T. p. columbianus*) and plains sharp-tailed grouse (*T. p. jamesi*; Connelly et al. 1998). While regional populations of sharp-tailed grouse have experienced significant declines, the plains subspecies is considered the most successful

with the broadest distribution (Hamerstrom and Hamerstrom 1961). However, populations of the plains subspecies have also declined, although populations remain strong in eastern Montana and parts of the Dakotas (Hamerstrom and Hamerstrom 1961, Yde 1977). While population declines are generally attributed to overgrazing and land conversion to cultivation (Yocom 1952, Hamerstrom and Hamerstrom 1961, Kessler and Bosch 1982), the relationship between human land use practices and sharp-tailed grouse populations is poorly understood (Kirsch et al. 1973). With large home ranges and differing requirements for nesting and winter habitat, sharp-tailed grouse require large and complex areas of habitat, making them an ideal umbrella species for grassland habitats (Roersma 2001, Spieles 2010). Sharp-tailed grouse are often seen as an indicator of quality rangeland (Hillman and Jackson 1973) and, therefore, identifying management actions for sharp-tailed grouse can have benefits for a suite of co-occurring species that use similar habitats.

Prairie Grouse Demography

Animal population dynamics are influenced by four vital rates: births and immigration, and deaths and emigration; and habitat selection is the individual decision-making process that links individual behavior to population abundance (Jones 2001, Boyce et al. 2016). In prairie grouse populations, births are a function of several parameters, including clutch size, egg hatchability and nest success, all of which influence fecundity, or the number of female chicks produced per adult female. Reproductive potential is typically high among prairie grouse, due to high rates of nesting, large clutch sizes, and high hatching rates (Bergerud and Gratson 1988a).

Therefore, early studies concluded that reproductive success would have the largest potential to influence prairie grouse population dynamics (Bergerud and Gratson 1988a, Wisdom and Mills 1997). Sensitivity analyses of populations of Columbian sharp-tailed grouse and lesser prairie-chickens (*T. pallidicinctus*) concluded that nest and brood survival had the largest impact on population dynamics, while female survival during the breeding period played a lesser role (Hagen et al. 2009, Gillette 2014). However, other studies found juvenile or adult survival to be more important determinants of population dynamics (McNew et al. 2012) and the relative importance of adult survival and fecundity varied among populations of greater prairie-chickens (*T. cupido*), suggesting that human land use patterns can affect the influence of vital rates on population dynamics, as well as the vital rates themselves (McNew et al. 2012).

Reproductive potential among grouse is high, with high rates of nest initiation, large clutch sizes, and high egg viability (Bergerud and Gratson 1988a). Nest survival can vary across years and sites for several reasons, including differences in weather, age structure of the population, predator populations and differences in available nesting cover (Bergerud and Gratson 1988a). In previous studies, sharp-tailed grouse nest success, or the probability of a nest hatching ≥ 1 egg, has varied from 0.32 in Utah (Hart et al. 1950) to 0.72 in Idaho (Meints 1991). Nest success can vary between first and re-nest attempts and is typically higher for adults than for yearling females (Bergerud and Gratson 1988a, Williamson 2009), although other studies have observed no difference in nest success between adult and yearling sharp-tailed grouse (Apa 1998, Collins 2004).

Nest site selection is critical for the reproductive success of female prairie grouse (Bergerud and Gratson 1988a). Ideal nesting habitat consists of high quality grasslands interspersed with shrubby cover (Hillman and Jackson 1973). Selection for specific fine-scale habitat characteristics by female sharp-tailed grouse varies throughout the range, as well as temporally within a single season. For example, shrubs may provide important concealment during initial nest attempts compared to subsequent attempts due to the increased amounts of herbaceous cover as the growing season progresses (Goddard and Dawson 2009). At the scale of both the nest site and the larger surrounding habitat patch, sharp-tailed grouse typically select for taller and denser vegetation, which provides both vertical and horizontal cover (Roersma 2001, Prose et al. 2002, Holloran et al. 2005, Manzer and Hannon 2005, Goddard et al. 2009). However, grouse often experience a tradeoff, as denser cover improves nest concealment but also increases the risk of predation for the female, which can result in selection for intermediate levels of cover (McNew et al. 2013).

Predation is responsible for the majority of nest failures in grouse, but the effects of predation are mediated by habitat conditions at the nest site (Bergerud and Gratson 1988a, Goddard and Dawson 2009). Therefore, habitat is considered to be the most important factor influencing nest survival and previous studies have found habitat characteristics at both the nest site and at larger spatial scales to be important predictors of nest survival (Manzer 2004, Goddard and Dawson 2009, McNew et al. 2013). Nest site selection is based primarily on characteristics that will reduce predation rates (Bergerud and Gratson 1988a, Connelly et al. 1998, Goddard and Dawson 2009) and the structural

diversity of vegetation, including height and density, are more important for habitat quality than the plant or floral species composition (Connelly et al. 1998, Roersma 2001). Structural diversity can provide sufficient hiding cover to minimize predation risk and concealment provided by shrubs, tall grasses, or residual cover from the previous year's herbaceous growth can be an important determinant of nest survival (Roersma 2001, Goddard and Dawson 2009). Nest cover is usually the most limiting factor for plains sharp-tailed grouse (Kessler and Bosch 1982) and nests of prairie grouse found in dense and tall cover are typically more successful (Manzer 2004, Pitman et al. 2006, Hagen et al. 2009). Cover provided by residual vegetation is especially critical for nesting prairie grouse because their nesting season starts before vegetation begins growing on the prairies. However, residual cover can be lacking on rangelands grazed by livestock (Bergerud and Gratson 1988a, Kirby and Grosz 1995, Prose et al. 2002). However, sharp-tailed grouse in North Dakota had higher nest success in areas grazed by cattle compared to ungrazed treatments (Kirby and Grosz 1995), so further research is necessary to identify optimal nesting habitat and management strategies (Roersma 2001).

While adult survival is influenced by a variety of factors, predation accounts for the majority of prairie grouse mortality (Bergerud and Gratson 1988a, Schroeder and Baydack 2001). Reported annual survival for sharp-tailed grouse ranges from 0.17-0.43 (Connelly et al. 1998), but was observed to be as high as 0.71 in South Dakota (Robel et al. 1972). Significant differences in survival between either adults and yearlings or between sexes have not been documented (Boisvert 2002, Collins 2004), but seasonal patterns and causes of mortality may differ between the sexes. Male mortality increases

during the lekking season when birds are conspicuous on communal leks, while increased female mortality can occur during the nesting season (Bergerud and Gratson 1988a).

Female lesser prairie-chickens attending nests or broods had lower daily survival rates than those without either a nest or brood (Hagen et al. 2007). However, periods of peak mortality depend on the severity of the winter. In Idaho, survival rates ranged from 0.86 in a mild winter to only 0.29 in a severe winter (Ulliman 1995).

Primary predators include coyote (*Canis latrans*), mink (*Mustela vison*), red fox (*Vulpes vulpes*), northern goshawk (*Accipiter gentilis*), gyrfalcon (*Falco rusticolus*), peregrine falcon (*Falco peregrinus*), rough-legged hawk (*Buteo lagopus*), northern harrier (*Circus cyaneus*), red-tailed hawk (*Buteo jamaicensis*), long-eared owl (*Asio otus*), and great horned owl (*Bubo virginianus*) (Connelly et al. 1998, Schroeder and Baydack 2001). Similar to nest survival, adult survival is influenced by local habitat factors and human land use practices. Survival of lesser prairie-chickens was greater in areas with higher vegetative cover and density (Patten et al. 2005). At a larger spatial scale, survival of female sharp-tailed grouse decreased in landscapes composed of more cropland (Manzer 2004). Grouse survival is typically negatively related to energy development and the corresponding increase in roads, fences and powerlines (Patten et al. 2005, Holloran et al. 2010). However, one study found an increase in greater prairie-chicken survival following the construction of a wind energy site, possibly mediated by the effect of the development on the local predator community (Winder et al. 2014a).

Habitat selection represents a link between individual behavior and population processes and can have important implications for population demography. The process

of habitat selection represents a trade-off between competing needs, such as acquiring resources for reproduction and avoiding predators to maximize fitness, and is a behavioral process through which individuals can respond to spatial and temporal variation in their environment. Habitat selection by grouse is primarily driven by predator avoidance, so having sufficient cover to conceal both nests and adults is important (Bergerud and Gratson 1988a). Grouse typically select for areas with greater horizontal and vertical cover (Marks and Marks 1987, Saab and Marks 1992, Goddard et al. 2009), more grassland on the landscape (Ryan et al. 1998, Niemuth 2003, Winder et al. 2015), and less cropland (Cope 1992, Manzer 2004, but see Goddard et al. 2009).

Grazing Management

Livestock grazing is the most widespread land management practice in the world and occurs on 70% of the land in western North America alone (Fleischner 1994, Krausman et al. 2009, Alkemade et al. 2013). As such, livestock grazing can have a significant impact on wildlife habitat. Grazing can directly affect ecosystem composition, function, structure, and productivity (Fleischner 1994, Boyd et al. 2014). For example, grazing can affect vegetation species composition through the active selection for specific plants by herbivores and the differential vulnerability of plants to herbivory (Fleischner 1994). Effects of grazing can either be positive or negative and are mediated by site conditions, including soil type, climate variables, and the plant community, as well as grazing management variables (Krausman et al. 2009). Grazing management variables can include the timing and intensity of stocking, livestock species, and the degree of active management, such as moving animals between pastures (Fleischner 1994).

Decreases in both the density and diversity of plant communities as a result of grazing have been documented in a variety of western ecosystems (Fleischner 1994), although trends in vegetation are often similar between ungrazed and moderately-to-lightly grazed areas and grazing can benefit plants during severe drought (Holechek et al. 2006). Impacts of grazing on native habitat can also vary with site potential, ecological condition, weather, and climate (Crawford et al. 2004). For example, clear negative effects of grazing, including shrub invasion and a decline in species diversity, have been recognized in some regions, while in others, native annual forb species richness and cover were higher in grazed areas (Hayes and Holl 2003). Grazing can also remove accumulations of standing dead vegetation, thus benefiting plant growth (Holechek et al. 2006). Furthermore, while grazing may be detrimental in arid regions, research in mesic areas suggests that grazing may be important to maintain historic disturbance regimes (Hayes and Holl 2003).

Range management often takes the form of season-long grazing, in which a single pasture is grazed for the entire season, from approximately May through November (Jefferies 1970). While there are advantages to season-long grazing, it can be difficult to prevent overgrazing in some years and preferred grasses are subjected to grazing during the same season in multiple years. Thus, it can be difficult to maintain key forage species (Jefferies 1970). Furthermore, studies suggest that season-long grazing may not maintain excellent range condition or at the very least will not improve degraded rangelands (Jefferies 1970, Watts et al. 1987, Krausman et al. 2009). Declines in range condition under season-long grazing and the widespread variation in grazing-rangeland

relationships related to differences in climate, vegetation, and soil type have led to the development of specialized grazing systems, including the Hormay rest-rotation system (Hormay and Evanko 1958), which are designed to improve range condition (Jefferies 1970). The rest-rotation system is based on the concept that grazing during the growing period over many years will lead to a reduction of plant vigor and that simply managing stocking rates will not result in proper grazing due to selective grazing by herbivores (Hormay 1970). Selective grazing can decrease both the abundance of specific plant species and overall range productivity, so rest from grazing is needed to allow plants to recover (Hormay and Evanko 1958, Hormay 1970). Rest-rotation systems are similar to other types of rotational grazing systems in that they incorporate the movement of stock between pastures to avoid grazing individual range units at the same time each year, but rest-rotation systems also include a rest period to allow for the preferred forage plants to periodically complete their growth cycle without defoliation (Hormay 1970). In addition, rest-rotation management explicitly incorporates grazing after seed ripe in order to improve recruitment and establishment of new seedlings by trampling seeds into the ground (Hormay and Evanko 1958). Rotational grazing could be useful for providing specific habitat elements for wildlife, such as food and cover, at specific places at a given time (Krausman et al. 2009). However, rest-rotation systems have several disadvantages over season-long grazing, including the need for more fences and water developments and increased movements of stock (Jefferies 1970, Holechek et al. 1999).

It is unclear whether rotational grazing systems, including rest-rotation, actually provide benefits to either vegetation or livestock production, and studies have found

conflicting results with regards to the effects of grazing systems on range condition (Krausman et al. 2009). Rest-rotation grazing increased forb abundance compared to areas ungrazed by livestock in Nevada (Neel 1980); improved vigor of key forage species, increased litter, and improved production of desirable grasses in eastern Montana (Willard and Herman 1977); and created similar vegetation conditions to ungrazed pastures in northcentral Montana (Watts et al. 1987). In contrast, pastures in southwestern North Dakota grazed season-long had significantly higher visual obstruction readings than those grazed with a deferred-rotation system (Mattise 1978). In addition, stocking rates have been shown to have consistently larger effects than particular grazing systems (Briske et al. 2008). For example, while herbage increased when specialized grazing systems, such as rest-rotation, were employed rather than season-long grazing, increases were much smaller than if stocking rates were decreased, suggesting that adjusting stocking intensities may have a greater effect than the implementation of grazing systems (Van Poollen and Lacey 1979).

Taken together, this suggests that no specific grazing system is best to meet specific conservation objectives, such as higher abundance of key forage species or higher visual obstruction, under all conditions or in all systems (Jefferies 1970). Responses of vegetation to grazing systems can differ by geographical region and can vary with local factors, including ecological condition of the site and climate variables (Van Poollen and Lacey 1979, Crawford et al. 2004). Furthermore, defining a level of ‘proper use’ of rangelands is also difficult, because a given level of utilization will have varying impacts on different plant species and grazing tolerance varies among species

and with climate conditions (Crawford et al. 2004, Boyd et al. 2014). Therefore, each grazing system should be tested under variable mediating conditions to determine the conditions for which it is best suited (Willard and Herman 1977).

Grazing and Wildlife

Overgrazing has been implicated in the decline of many different wildlife populations (Fleischner 1994), but studies examining the effects of grazing on wildlife populations are limited and even fewer have examined the effects of specialized grazing systems (Grosz and Kirby 1986, Krausman et al. 2009). Livestock can impact wildlife directly, such as through the trampling of nests, or indirectly, through effects on habitat structure and prey availability (Fleischner 1994). Many grassland species co-evolved with large grazing animals and different species of grassland birds, for example, require habitats along the entire structural gradient from relatively undisturbed vegetation to very short vegetation associated with heavy grazing (Samson and Knopf 1996, Derner et al. 2009). As a result, bird species diversity is often higher in grasslands managed for heterogeneity than in areas managed with intensive early stocking systems that promote uniform utilization (Coppedge et al. 2008), although accumulating evidence suggests that stocking rates and precipitation are more important and mediate the impacts of specific grazing systems (Briske et al. 2008, Lipsey and Naugle 2017, Vold 2018). Grazing could therefore be a useful management technique to diversify habitats and provide a mosaic of patches in different stages of recovery from disturbance by livestock (Ryder 1980, Fuhlendorf and Engle 2001, Coppedge et al. 2008, Krausman et al. 2009). Habitat requirements of prairie grouse encompass the full range of vegetation structure, with

short, bare areas used for lekking; denser, herbaceous cover for nesting; and thicker shrubs for winter cover and food (Marks and Marks 1988, Derner et al. 2009). As a result, prairie grouse are recognized as indicator species for grassland habitats and, therefore, identifying appropriate grazing management strategies to conserve grouse populations could have implications for a suite of grassland species (Hillman and Jackson 1973, Poiani et al. 2001, Roersma 2001).

Declines of many prairie grouse populations have been linked to poor grazing management (Ryder 1980, Giesen and Connelly 1993), and, while several studies suggest that grazing can have potentially beneficial effects on grouse habitat, few researchers have examined direct links between grazing management and grouse demography (Crawford et al. 2004, Boyd et al. 2014, Dettenmaier et al. 2017). If managed inappropriately, livestock grazing can be detrimental to prairie grouse, particularly through the removal of residual cover necessary for nesting and brood-rearing and through the degradation of winter riparian habitat (Giesen and Connelly 1993, Stinson and Schroeder 2012). Several studies have documented the removal of critical perennial grass cover due to heavy grazing and resultant declines of both lesser and greater prairie-chickens (Ryder 1980). Sustained heavy grazing can also favor annual grasses and thus reduce the perennial grasses that provide optimal cover (Crawford et al. 2004, Boyd et al. 2014). Another important negative effect of excessive grazing is the loss or damage of deciduous riparian habitat. If not managed, cattle often spend a disproportionate amount of time in riparian areas, which can concentrate both excessive grazing and trampling and reduce deciduous shrubs and trees that provide necessary winter cover and food (Kessler

and Bosch 1982, Nielsen 1982, Giesen and Connelly 1993). In addition to effects on habitat, grouse may simply avoid areas with heavy grazing, which could lead to increased nest abandonment and decreased lek attendance, although other studies suggest that high site fidelity may cause grouse to remain in the same area despite intensive grazing (Holechek et al. 1982, Nielsen 1982, Crawford et al. 2004).

If managed appropriately, however, specialized grazing systems could benefit prairie grouse, particularly by emphasizing heterogeneity-based management practices (Fuhlendorf and Engle 2001, Derner et al. 2009). In the tallgrass prairie, for example, patch-burn grazing is employed as a heterogeneous management technique to create a patchwork of grassland habitats (Fuhlendorf and Engle 2001). Patch-burn grazing increased both nest success and adult survival of greater prairie-chickens and altered patterns of habitat selection in comparison to intensive early stocking, which incorporates similar stocking rates to season-long systems but concentrates grazing activity during the first half of the growing season (McNew et al. 2015, Winder et al. 2017, Winder et al. 2018). Rotational grazing systems, such as the Hormay rest-rotation system, could function similarly to increase habitat heterogeneity in the absence of fire in order to meet the range of prairie grouse habitat requirements (Hormay and Evanko 1958, Frisina 1991, Montana Department of Fish, Wildlife & Parks 2011). The rest-rotation system was developed in response to widespread declines in range condition and is based on the idea that, without periodic rest from grazing during the growing season, livestock grazing can decrease both the abundance of specific plant species and overall range productivity (Hormay and Evanko 1958, Hormay 1970). While the original intent was to improve

range condition, rest-rotation grazing could create pasture-level heterogeneity on the landscape with a range of habitat conditions including increased residual cover in pastures that were rested the previous year (Frisina 1991, Montana Department of Fish, Wildlife & Parks 2011). In Montana, a rotational grazing system provided additional nesting and brood-rearing cover for waterfowl, and in South Dakota, sharp-tailed grouse preferentially nested in rested pastures (Gjersing 1975, Rice and Carter 1982 in Krausman et al. 2009), although a study in central Montana found only weak effects of rotational grazing management on both vegetation and greater sage-grouse (*Centrocercus urophasianus*) nest survival (Smith et al. 2018a;b). In addition, the timing of grazing can have divergent effects on plant communities. Heavy grazing early in the spring can have several negative effects, such as the removal of residual vegetation, but can also stimulate new growth, while grazing in the late summer to fall can actually increase both perennial grasses and forbs (Crawford et al. 2004). Under rest-rotation grazing, pastures are not grazed at the same time every year, which could mitigate some of the negative effects of grazing during particular seasons and create heterogeneity, with the pastures rested in the previous year having the most residual cover. However, effects of grazing systems are also mediated by stocking rate, with high stocking rates consistently shown to have negative effects on grouse populations (McNew et al. 2015, Kraft 2016, Winder et al. 2018).

While many studies have examined the effects of grazing systems on vegetation and linked that to potential impacts on grouse habitat, the postulated effects of grazing on grouse populations remain limited in both the number of species and systems studied

(Dettenmaier et al. 2017). No studies have examined the direct effects of grazing on either sharp-tailed grouse demography or habitat selection and related fitness costs. While increased habitat heterogeneity is thought to benefit grouse, any advantages depend on the scale at which the heterogeneity is relevant to the grouse. For example, rested pastures within a rest-rotation system could provide good cover compared to the less heterogeneous utilization in the grazed pastures, thus creating heterogeneity on a pasture scale, while season-long grazing could create a patchwork of structure within a large pasture (Yde 1977, Mattise 1978). Furthermore, vegetation and wildlife responses to grazing management can vary relative to both regional and local factors, such as soil type and climate (Van Poollen and Lacey 1979, Crawford et al. 2004, Lipsey and Naugle 2017). While certain grazing regimes can negatively affect wildlife habitat, properly managed grazing can be compatible with wildlife conservation (McNew et al. 2015, Winder et al. 2018) and is preferable to other land uses that destroy or fragment native grasslands (Deeble 1996). Maintaining ranching economies in which grasslands are well managed offers the most viable conservation strategy for preserving grassland wildlife (Krausman et al. 2009). Therefore, research is needed to evaluate the direct effects of grazing on grouse populations to develop appropriate conservation strategies that produce high quality wildlife habitat while providing viable income for livestock producers.

The primary objective of this study was to examine the effects of rangeland management on sharp-tailed grouse ecology and assess whether rest-rotation grazing is a management technique that is compatible with healthy, sustainable populations of sharp-tailed grouse in the northern mixed-grass prairie. In Chapter 2, I evaluate the effects of

rangeland management on the nesting ecology of sharp-tailed grouse. In Chapter 3, I assess the effects of grazing management on the seasonal survival and spatial mortality risk of adult sharp-tailed grouse. In Chapter 4, I examine the effects of rangeland management on the breeding season space use and habitat selection of female sharp-tailed grouse. In Chapter 5, I provide conclusions from my research and management recommendations for improving habitat for sharp-tailed grouse, an indicator species for grassland ecosystems.

CHAPTER TWO

EFFECTS OF RANGELAND MANAGEMENT ON THE NESTING ECOLOGY OF
SHARP-TAILED GROUSE

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CHAPTER TWO

EFFECTS OF RANGELAND MANAGEMENT ON THE NESTING ECOLOGY OF
SHARP-TAILED GROUSE**INTRODUCTION**

Grasslands are a globally important ecosystem, covering an estimated 25–40% of the terrestrial planet and providing critical habitat for a variety of plants and animals (White et al. 2000, Boval and Dixon 2012, Blair et al. 2014). Despite their array of benefits, temperate grasslands are one of the ecosystems most altered by human activity and suffering from the greatest levels of habitat loss and degradation (Hoekstra et al. 2005, MEA 2005). Mixed-grass prairies, in particular, have lost most of their original land, with only an estimated 25–30% of historic prairie intact (Johnson and Bouzaher 1995, Askins et al. 2007). Losses of grassland habitat can have serious repercussions, including the decline and extirpation of populations, changes in ecosystem function, and the deterioration of ecosystem services (Ceballos et al. 2010). Grassland birds, for example, have experienced more significant and widespread declines in the past decades than any other guild of birds in North America (Knopf 1994).

Livestock grazing is the most widespread land management practice in the world, occurring on 70% of the land in western North America alone (Fleischner 1994, Krausman et al. 2009, Alkemade et al. 2013), and can directly affect ecosystem composition, function, structure, and productivity (Fleischner 1994, Boyd et al. 2014). Range management often takes the form of season-long grazing, in which a single pasture is grazed for the entire growing season (Jefferies 1970). While there are advantages to

season-long grazing, it can be difficult to prevent overgrazing in some years and preferred grasses are repeatedly subjected to grazing during the same season, making it difficult to maintain key forage species (Jefferies 1970). Declines in range condition under season-long grazing and widespread variation in the grazing-rangeland relationship related to differences in climate, vegetation, and soil type have led to the development of specialized grazing systems, including the Hormay rest-rotation system (Hormay and Evanko 1958). This system is based on the concept that repeated grazing during consecutive growing seasons will lead to a reduction of plant vigor over many years, and that simply managing stocking rates will not result in proper grazing due to selective grazing by herbivores. Repeated grazing can decrease both the abundance of specific plant species and overall range productivity (Hormay and Evanko 1958, Hormay 1970). Rest-rotation systems incorporate the movement of livestock between pastures to avoid grazing individual range units at the same time each year, and include a rest period to allow for the regrowth of vegetation (Jefferies 1970). While rest-rotation grazing was developed to improve range condition, it could conceptually be beneficial for wildlife conservation based on its potential to provide pasture-level heterogeneity on the landscape (Frisina 1991). However, its utility for improving habitat for wildlife in the mixed-grass prairie has rarely been directly evaluated and results relating specific grazing systems to vegetation have varied widely, even within a single grassland ecosystem (Krausman et al. 2009).

Overstocking has been broadly implicated in the decline of many different wildlife populations (Fleischner 1994), but few studies have examined the effects of

specialized grazing systems (Grosz and Kirby 1986, Krausman et al. 2009). Livestock can impact wildlife directly, such as through the trampling of nests, or indirectly, through effects on habitat structure and prey availability (Fleischner 1994). Many grassland species co-evolved with large grazing animals and different species of grassland birds, for example, require habitats along the entire structural gradient from relatively undisturbed vegetation to very short vegetation associated with heavy grazing (Samson and Knopf 1996, Derner et al. 2009). As a result, bird species diversity is often higher in grasslands managed for heterogeneity than in areas managed with traditional uniform grazing or fire disturbance (Coppedge et al. 2008). Certain grazing regimes could therefore be useful management techniques to diversify habitats and provide a mosaic of patches in different stages of recovery from disturbance by livestock (Ryder 1980, Fuhlendorf and Engle 2001, Coppedge et al. 2008, Krausman et al. 2009).

Sharp-tailed grouse (*Tympanuchus phasianellus*) are a model species to evaluate the effects of grazing management regimes on grassland wildlife. Habitat requirements of sharp-tailed grouse encompass the full range of vegetation structure, with short, bare areas used for lekking; denser, herbaceous cover for nesting; and thicker shrubs for winter cover and food (Derner et al. 2009). As a result, prairie grouse (*Tympanuchus* spp.), including sharp-tailed grouse, are recognized as indicator species for grassland habitats and, therefore, identifying appropriate grazing management strategies to conserve grouse populations could have implications for a suite of grassland species (Hillman and Jackson 1973, Poiani et al. 2001, Roersma 2001).

Poor range management has been implicated in the decline of sharp-tailed grouse throughout North America (Johnsgard 1983), but the effects of specific grazing regimes on grouse populations have not been studied (Dettenmaier et al. 2017). Therefore, a better understanding of the ecological impacts of different grazing systems is required to develop effective conservation strategies. Our objectives were to evaluate rest-rotation grazing as a conservation management technique compared to more traditional grazing systems, including summer rotation and season-long grazing, and assess the effects of different grazing systems and stocking rates on both nest site selection and nest survival of sharp-tailed grouse in the mixed-grass prairie. As ground-nesting birds, most reproductive losses of sharp-tailed grouse are caused by predation of nests and young, and vegetation conditions providing both protective and thermal cover are typically critical to nest survival (McNew et al. 2012, Hovick et al. 2014a, McNew et al. 2014). Grazing systems, such as rest-rotation, that periodically rest portions of the landscape from disturbance may result in heterogeneous habitat conditions that could improve overall reproductive success due to increased availability of vegetation cover for nesting. Therefore, we hypothesized that female sharp-tailed grouse would both select nest sites in pastures managed with rest-rotation grazing and experience higher rates of nest survival in those pastures if rest-rotation grazing created pasture-level differences in vegetation conditions.

METHODS

Study Area

Our study was conducted in southern Richland and McKenzie Counties in eastern Montana and western North Dakota, respectively, during 2016–2018 (Fig. 1). The study area was primarily managed for cattle production and composed of Great Plains mixed-grass prairie interspersed with Great Plains badlands and wooded draws and ravines (LANDFIRE 2013). The vegetation was a mixture of mid and short grasses, with the dominant native graminoids including western wheatgrass (*Pascopyrum smithii*), little bluestem (*Schizachyrium scoparium*), needle-and-thread (*Hesperostipa comata*), and blue grama (*Bouteloua gracilis*), and non-native graminoids including Kentucky bluegrass (*Poa pratensis*) and crested wheatgrass (*Agropyron cristatum*).

The study area was centered on an ~3,300-ha Upland Gamebird Enhancement Program (UGBEP) project established by the Montana Department of Fish, Wildlife, and Parks in 1993 that includes four separate 3-pasture Hормay rest-rotation systems (Hormay and Evanko 1958). Within each 3-pasture rest-rotation management unit, cattle were stocked in one pasture from May–July in the first year (growing season), then moved to the second pasture during August–October (post-growing season), and the third pasture was rested. The order of rotation was then rotated the next year so that no pasture was grazed during the same season in consecutive years and that pastures rested in the previous year theoretically should have the most residual cover. Average pasture size in the rest-rotation system was 292 ± 116 ha. Pastures of surrounding ranches, including both private land and 4 pastures located on U.S. Forest Service National Grasslands, were

managed with more commonly used livestock grazing systems, including both season-long systems (19 pastures, ~4,800 ha) and 2- and 3-pasture summer rotation systems (25 pastures, ~5,200 ha). Season-long pastures allowed grazing from approximately May to early November, while summer rotation systems stocked cattle in the same pastures each year for the same 6–8-week period (approximately April–June, June–July or Aug–Nov). Average pasture sizes in the season-long and summer rotation systems were 242 ± 312 ha and 238 ± 335 ha, respectively. Stocking rates were controlled by landowners and lessees and averaged rates were 0.93 AUM ha^{-1} , 1.46 AUM ha^{-1} , and 0.76 AUM ha^{-1} for rest-rotation, season-long, and summer rotation pastures, respectively. The range of stocking rates for grazed pastures was $0.38 - 3.25 \text{ AUM ha}^{-1}$, $0.17 - 4.28 \text{ AUM ha}^{-1}$, and $0.21 - 4.45 \text{ AUM ha}^{-1}$ for rest-rotation, season-long, and summer rotation pastures, respectively, and included similar distributions within each grazing system (see Appendix A).

Environmental variables, including topography, average vegetation productivity, soil type, and vegetation canopy greenness as measured by the Normalized Difference Vegetation Index (NDVI) in June 2018, were similar among grazing systems (Table 1).

Field Methods

We captured grouse during March–May at 12 leks (5 in rest-rotation pastures, 3 in summer rotation pastures and 4 in season-long pastures) using walk-in funnel traps. Females were fitted with very high frequency (VHF) radio-transmitters (model A4050; Advanced Telemetry Systems, Isanti, MN). Radio-marked females were located by triangulation or homing ≥ 3 times/week during the nesting period (April–July). When females localized in an area, we assumed that the female was attending a nest. 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 Global Position System (GPS) unit. Nests were only approached under dry conditions and observers wore rubber boots and walked in circles to avoid leaving a direct scent trail to the nest. Nests were subsequently approached 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, based on eggshell remains, predator sign, or female behavior. All animal handling was approved under Montana State University's Institutional Animal Care and Use Committee (Protocol #2016-01).

We evaluated habitat conditions at each nest site within 3 days of hatching or expected hatch date in the case of failure (Gibson et al. 2016). 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 (Connelly et al. 1998). Random points that fell within non-habitat (i.e., water, cultivation, etc.) or were located on properties to which we did not have access were replaced. 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, McNew et al. 2013). 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 following Daubenmire (1959).

We also measured nest habitat at the home range scale (500 ha, based on estimated home range sizes of sharp-tailed grouse during the breeding season, M. C. Milligan, unpublished data). 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 proportion of grassland, the density of edge habitat (total landcover edge length / polygon area), and mean shape complexity (MSI) within a 500-ha polygon centered on the nest or random point. Mean shape complexity 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. We also digitized the locations of oil pads and roads which represented the major forms of disturbance in the study area and calculated the distance to the nearest oil pad or road from each point.

We gathered 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. We then calculated the following grazing management variables: grazing system (rest-rotation, summer rotation, season-long), stocking rate (AUM ha⁻¹), and stocking density during the nest attempt (AU ha⁻¹). Stocking rate is a measure of the number of animals in a grazing unit during the entire grazing season, whereas stocking density during the nest attempt is a relative index of cow use during the period when the nest was active. Analyses evaluated stocking rate from both the previous and current year's grazing.

Statistical Analyses

Nest Site Selection

We examined habitat and management variables influencing nest site selection in separate analyses using resource selection functions (RSFs). 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 AIC_c and model selection was based on both minimization of AIC_c and AIC_c 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 in 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).

Nest Survival

Nest success is defined as the probability of a nest producing ≥ 1 chick, whereas nest survival accounts for potential losses of nests before discovery (Dinsmore et al. 2002). We constructed nest survival models for Program MARK 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, Laake 2013).

Similar to the nest site selection analysis, we evaluated models of daily nest survival at both the habitat and management levels 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, daily temperature, and three precipitation variables compared to a null model of constant daily nest survival (Goddard and Dawson 2009). Female condition was calculated by regressing body mass adjusted for capture date against the length of the wing chord using the reduced major axis method (Green 2001). We evaluated both daily precipitation with a 1-day time lag to examine potential increased predation following precipitation events (Lehman et al. 2008), and cumulative precipitation measures, including 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), to evaluate inter-annual

differences in precipitation that could be driving variability in vegetation growth. We then selected the most parsimonious models at each of the different scales and assessed them in the final candidate model set using AIC_c. 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 and additive models with stocking density, stocking rate and year. We then evaluated a final candidate model set with combinations of important variables from both the habitat- and management-level analyses to assess the relative importance of each variable.

We then subsetted the nest data and selected only nests occurring in rest-rotation pastures. We developed a separate set of candidate models to examine the effects of grazing variables on nests within the rest-rotation pastures 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). Analyses used the treatment from the previous year's grazing season rather than the current year, because we were evaluating effects on nesting ecology as mediated through the effects of grazing on vegetation variables and the previous year's treatment has the largest effect on the amount of residual cover available to nesting grouse the following 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 area (37-d). Variance of overall nest survival was estimated with the delta approximation method (Seber 1982). The average duration of the egg-laying and

incubation periods (37-d) was determined from observations of our sample of successful nests and from previous work (Connelly et al. 1998).

Habitat Conditions

We tested the effects of grazing management on habitat conditions using generalized linear models. We restricted our analyses to habitat variables found to be important for grouse nest site selection and survival and tested the relationships between those variables and both grazing system and stocking rate (AUM ha^{-1}). We used generalized linear models with a gamma error structure to create a set of candidate models and models were compared using AIC_c ; models with large model weights (w_i) and AIC_c values ≤ 2 from the best-fit model were considered equally parsimonious (Burnham et al. 2011).

RESULTS

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 (see Appendix B). At the nest-level, nest site selection was best predicted by VOR at the nest bowl and the percentage of new grass, residual grass, and shrubs ($\Delta\text{AIC}_c = 0$, $w_i = 0.61$). At the home-range level,

the model containing a measure of fragmentation (mean shape complexity or MSI) received the most support ($\Delta\text{AIC}_c = 0$, $w_i = 0.56$). In the final candidate model set, the model that included VOR at the nest bowl, the percentage residual grass, and MSI received the most support ($\Delta\text{AIC}_c = 0$, $w_i = 0.61$, Table 2). Confidence intervals for VOR, MSI, and proportion residual grass and shrubs did not overlap zero, suggesting significant effects (Fig. 2). Percent cover of both residual grass ($\beta = 0.48 \pm 0.17$) and shrubs ($\beta = 0.33 \pm 0.20$) had small but positive effects on the relative probability of selection, while selection decreased with increasing fragmentation or MSI ($\beta = -0.50 \pm 0.16$). Visual obstruction at the nest bowl had the largest effect on the relative probability of selection ($\beta = 11.45 \pm 1.31$), with selection increasing up to a threshold of 20–30 cm (Fig. 2).

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 2), with 85% confidence intervals that did not overlap zero. The relative probability of selection declined with increasing stocking rates ($\beta = -0.17 \pm 0.10$). However, in the full analysis, the model containing habitat variables ($\Delta\text{AIC}_c = 0$, $w_i = 0.58$) outperformed models with management-level variables (Table 2), 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 ($R^2 = 0.87$).

Nest Survival

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). 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 ($\Delta\text{AIC}_c = 0.50 - 1.83$, $w_i = 0.13 - 0.26$) and so were examined in the final model set. At the home-range level, distance to road received the most support ($\Delta\text{AIC}_c = 0$, $w_i = 0.35$) and proportion grassland marginally improved model fit compared to the null model ($\Delta\text{AIC}_c = 1.36$, $w_i = 0.18$), so both variables were included in the final analysis. In the final candidate model set, the model that included VOR, percentage forbs and proportion grassland received the most support ($\Delta\text{AIC}_c = 0$, $w_i = 0.43$, Table 3). VOR was in all twelve top models, accounting for 100% of the relative support of the data, while proportion grassland accounted for 79% of relative support. Confidence intervals for VOR, proportion grassland, and distance to road did not overlap zero, indicating significant effects (Fig. 3). Daily nest survival increased with proportion grassland ($\beta = 0.16 \pm 0.10$), distance to road ($\beta = 0.21$

± 0.11), and VOR up to a threshold of 20–30 cm, as represented by the pseudo-threshold model ($\beta = 0.29 \pm 0.11$).

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 ($\beta = 0.30 \pm 0.14$, Fig. 4). 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 ($\beta = 0.36 \pm 0.25$) and 2018 ($\beta = 0.73 \pm 0.28$) than in 2016 and was lower in rest-rotation pastures compared to season-long pastures ($\beta = -0.44 \pm 0.27$). Overall nest survival (\pm SE) was 0.48 ± 0.07 in season-long pastures, 0.38 ± 0.06 in summer rotation pastures, and 0.32 ± 0.06 in rest-rotation pastures (Fig. 5). In the full analysis, the model with the most support included VOR, proportion grassland and stocking density while the nest was active ($\Delta AIC_c = 0$, $w_i = 0.90$, Table 3), with confidence intervals for all three variables not overlapping zero, suggesting significant effects.

For nests within the rest-rotation system ($n=57$), there was no evidence for an effect of the timing of grazing (grazed during the growing season, grazed post-growing season, or rested entire year) on nest survival (Table 4). Estimates of overall nest survival in the three treatments overlapped entirely (Fig. 5).

Habitat Conditions

We evaluated the effects of management-level variables on VOR measured at the nest bowl and averaged within the 6 m radius plot, because those were the most important variables in the nest site selection and nest survival analyses, respectively. Stocking rate best predicted VOR at the nest bowl ($\Delta\text{AIC}_c = 0$, $w_i = 0.45$, Table 5) and had a negative effect ($\beta = -0.06 \pm 0.02$). An additive effect of grazing system and stocking rate was the best predictor of average VOR in the 6 m radius plot ($\Delta\text{AIC}_c = 0$, $w_i = 0.49$, Table 5). Stocking rate had a negative effect on average VOR ($\beta = -0.10 \pm 0.03$) and VOR was consistently lower in the rest-rotation system compared to either the season-long or summer rotation systems. However, variation in visual obstruction was larger within each grazing system than observed differences among systems (Fig. 6).

DISCUSSION

Both nest site selection and nest survival were strongly associated with visual obstruction, an index of nest concealment and biomass (Robel et al. 1970) that is also related to thermal stress mitigation (Hovick et al. 2014a). Grazing system influenced visual obstruction, but variation within each grazing system was larger than differences among systems, suggesting that the rest-rotation system was not enhancing pasture-level heterogeneity relative to other grazing systems, with inherent landscape variability outweighing any effects of grazing system to influence heterogeneity at the spatial scale relevant to nesting grouse. However, stocking rate indirectly influenced nest survival through effects on visual obstruction and stocking density while the nest was active

improved nest survival, possibly due to the mitigating presence of cows or ranchers on nest predators.

Both nest site selection and nest survival were strongly influenced by vertical structure of vegetation cover and exhibited an asymptotic relationship with visual obstruction, with the relative probability of selection and daily survival increasing up to 20–30 cm. Previous studies have supported the strong effect of visual obstruction on nesting prairie grouse (Manzer and Hannon 2005, Pitman et al. 2005, McNew et al. 2015). Although results differ regarding the functional relationship between visual obstruction and nest survival, our work combined with previous studies suggest that a minimum of 20–30 cm of vertical cover within 6 m of the nest bowl is optimal for most prairie grouse.

We found that grazing system did not significantly influence nesting sharp-tailed grouse, but stocking rate had indirect effects on nesting ecology through impacts on vegetation cover. In the management-level analyses, stocking rate and grazing system influenced nest site selection and nest survival, respectively, but both were outweighed by the effects of small-scale habitat variables. Our analysis of the effects of grazing management on habitat conditions suggests that stocking rate can have a biologically meaningful influence on visual obstruction, while effects of grazing system were minimal, which concurs with previous reviews of rangeland management approaches (Briske et al. 2008, Briske et al. 2011). Previous studies that found an effect of grazing management on nest site selection or nest survival have also either found a strong link between grazing variables and local habitat, including visual obstruction, or have only

evaluated grazing management without controlling for habitat variables (McNew et al. 2015, Kraft 2016). Our results are more consistent with a study in central Montana that found negligible effects of grazing management on vegetation variables and only weak effects on greater sage-grouse (*Centrocercus urophasianus*) nest survival (Smith et al. 2018a;b). While we found evidence that stocking rate and grazing system influenced visual obstruction, differences among systems were relatively small, particularly compared to within-system variation. Furthermore, results were consistent across years, despite large differences in precipitation. Therefore, grazing system may be a relatively minor driver of heterogeneity in vertical cover in our study area, although stocking rates were moderate across the study area (≤ 2.0 AUM ha⁻¹), which could mediate responses from prairie grouse.

Previous work has found that management practices that resembled historic disturbance regimes and focused on providing pasture-level heterogeneity in vegetation structure and composition are key to maintaining natural ecosystem processes and can improve reproductive success of ground-nesting birds like grouse (Fuhlendorf and Engle 2004, McNew et al. 2015). Similarly, rest-rotation grazing is thought to improve wildlife habitat by creating heterogeneity at the pasture scale (Frisina 1991), but our research suggests that it did not increase heterogeneity at a spatial scale relevant to nesting sharp-tailed grouse relative to other grazing systems. We found no evidence for a statistically meaningful difference in nest survival among the three treatments within the rest-rotation system, suggesting that it was not influencing pasture-level heterogeneity in the vegetation cover required by nesting grouse. At moderate stocking rates like those found

in our study area (≤ 2.0 AUM ha⁻¹), the selective foraging of cattle can create a patchwork of small heavily grazed patches and ungrazed or lightly grazed patches within a single pasture (Bailey et al. 1998, Fuhlendorf and Engle 2001). Selective grazing by cattle stocked at moderate stocking rates in rangelands with inherent topographical and edaphic variation naturally creates significant vegetation heterogeneity within a pasture regardless of grazing system. We found strong evidence that grouse were selecting nest sites within their home ranges at a very small spatial scale based on vegetation cover at the nest bowl itself, which coincides better with patch-scale heterogeneity created by selective foraging than the larger-scale pasture-level heterogeneity potentially created by rest-rotation grazing.

While grazing system did not have a strong effect on nesting ecology as mediated through vegetation variables, we did find a direct relationship between stocking density while the nest was active and nest survival, which is inconsistent with previous research (Smith et al. 2018a). Previous studies evaluating the effects of grazing management on grouse have either used indirect measures of cattle use such as dung pat surveys (Smith et al. 2018a) or focused on indirect impacts of grazing activity on vegetation and how that can affect nest survival, measuring stocking rates or densities for the entire grazing period rather than during the period while the nest was active (McNew et al. 2015, Kraft 2016). In contrast, our results suggest that having cow-calf pairs in a pasture while nests were active can have a positive effect on nest survival, potentially through an effect on predator behavior, which coincides with a study on greater sage-grouse in southeastern Montana (Foster et al. 2015). Pastures in our study area were primarily stocked with cow-

calf pairs and previous research found that cows with calves are significantly more vigilant than those without calves, potentially resulting in behavior that causes predators to avoid pastures that have higher densities of cows (Kluever et al. 2008, Foster et al. 2015). In addition, ranchers may spend more time checking pastures with more livestock, thus also acting as a deterrent to predators. However, stocking densities in our study area were relatively low ($\leq 1.3 \text{ AU ha}^{-1}$ while nests were active) and the positive effect may not hold at higher stocking densities, where the positive benefits of cow presence could be offset by indirect negative effects on nesting cover.

IMPLICATIONS

Livestock grazing is a predominant land use worldwide and can have huge potential impacts on the ecosystem functioning of native grasslands (Fleischner 1994, Boyd et al. 2014). Furthermore, the majority of the remaining mixed-grass prairie is found on land managed for livestock production, so conservation strategies for grassland wildlife will necessitate appropriate grazing management strategies. Rest-rotation grazing was originally developed to promote the recovery of sensitive bunchgrass species in the Great Basin, but could function conceptually as a conservation-focused management strategy to promote pasture-level heterogeneity (Hormay and Evanko 1958, Frisina 1991). However, our results suggest that rest-rotation grazing did not increase pasture-level heterogeneity relative to other grazing systems or influence vegetation heterogeneity at a spatial scale relevant to nesting grouse in northern mixed-grass prairies. Both nest site selection and nest survival were strongly associated with vertical cover at a small grain size, and while grazing systems did create variation in visual obstruction, that variation was outweighed

by natural variability across the landscape. The selective foraging of cattle likely contributed more to heterogeneity at a spatial scale relevant to nesting sharp-tailed grouse, because females were selecting nest sites at a very small spatial scale. However, caution should be exercised when extrapolating our results outside of the northern mixed-grass prairie. Previous research suggests that demographic responses of grouse can vary due to interactions between grazing management and primary productivity across large spatial scales (Monroe et al. 2017). Therefore, nesting sharp-tailed grouse responses in regions with higher stocking rates or less inherent landscape variability may differ from those found in our study.

Our results suggest that management interventions such as alternative grazing strategies may not have significant benefits for sharp-tailed grouse productivity in the northern mixed-grass prairie. Where land is predominantly under private ownership, cropland conversion represents the most significant threat to grassland wildlife (Hoekstra et al. 2005, Stephens et al. 2008). Therefore, economically viable ranching strategies with moderate stocking rates that keep native grasslands on the landscape should be prioritized over specific grazing management systems.

Table 1. Environmental variables summarized by grazing system. Productivity and soil classifications were obtained from published ecological site descriptions from the Natural Resources Conservation Service (NRCS). Normalized Difference Vegetation Index (NDVI) was calculated from Landsat 8 imagery and represents a measure of vegetation canopy greenness.

System	Avg. slope	Prod (kg/ ha)	% Limy residual	% Shallow loamy	% Silty-Steep	% Silty	Avg. NDVI	Min. NDVI	Max. NDVI
Rest-rotation	5.73 ± 3.69	1582 ± 615	2.9	8.7	49.1	34.8	0.28 ± 0.06	-0.06	0.56
Summer rotation	4.62 ± 3.30	1936 ± 620	31.4	18.2	5.5	20.9	0.31 ± 0.06	-0.02	0.63
Season-long	4.99 ± 3.54	1954 ± 631	17.9	13.2	11.7	29.2	0.31 ± 0.07	-0.06	0.5

Table 2. Support for final candidate models evaluating sharp-tailed grouse nest site selection in 2016–18 in the three analyses examining habitat-level variables, management-level variables, and the combined analysis. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and log-likelihoods are reported. VOR is visual obstruction as measured at the nest bowl and mean shape complexity (MSI) is a measure of patch shape irregularity and is defined as the sum of each landcover patch's perimeter divided by the square root of each patch area and divided by the number of patches, such that it equals 1 when all patches are circular.

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

Stocking Rate (prv. yr)	3	526.45	0.00	0.26	0.26	-260.19
Stocking Rate (prv. yr) + Grazing System	5	526.54	0.09	0.25	0.51	-258.19
Null	2	528.04	1.59	0.12	0.63	-262.00
Stocking Rate (cur. yr)	3	528.49	2.05	0.09	0.73	-261.22
Grazing System	4	528.90	2.45	0.08	0.81	-260.40
Stocking Rate (cur. yr) * Grazing System	7	529.71	3.26	0.05	0.86	-257.70
Stocking Rate (cur. yr) + Grazing System	5	529.85	3.40	0.05	0.90	-259.85
Grazing System * Stocking Rate (prv. yr)	7	530.34	3.89	0.04	0.94	-258.02
Stocking Rate (prv. yr) + Year	5	530.51	4.06	0.03	0.98	-260.17
Stocking Rate (cur. yr) + Year	5	532.47	6.02	0.01	0.99	-261.16
Grazing System + Year	6	533.02	6.57	0.01	1.00	-260.40
Grazing System * Year	10	541.07	14.62	0.00	1.00	-260.24
Full Analysis						
ln(VOR) + %Residual + MSI	5	284.95	0.00	0.58	0.58	-137.40
ln(VOR) + %Residual + MSI + Stocking Rate (prv. yr.)	6	285.57	0.61	0.42	1.00	-136.67
Stocking Rate (prv. yr.)	3	526.45	241.49	0.00	1.00	-260.19
Null	2	528.04	243.09	0.00	1.00	-262.00

Table 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
Habitat Analysis					
ln(VOR) + %Forb + Prop. Grassland	4	747.50	0.00	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	745.70
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

In(VOR) + %Forb	3	754.09	6.59	0.02	748.08
In(VOR) + %Residual	3	755.41	7.91	0.01	749.41
In(VOR) + %New Grass	3	755.42	7.92	0.01	749.42
Dist. to Road	2	757.17	9.68	0.00	753.17
Prop. Grassland	2	758.53	11.03	0.00	754.53
Null	1	758.94	11.44	0.00	756.94

Management Analysis

Stocking Density	2	755.05	0.00	0.24	751.05
Stocking Rate (cur. yr.) + Year + Stocking Density	5	755.10	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	757.20	2.15	0.08	749.19
Stocking Rate (prv. yr.) + Year	4	757.30	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	760.90	5.85	0.01	756.89
Stocking Rate (cur. yr.) + Grazing System	4	761.85	6.80	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	0.00	745.19
Stocking Rate (cur. yr.) * Grazing System	6	765.83	10.78	0.00	753.81
Stocking Rate (prv. yr.) * Grazing System	6	765.84	10.79	0.00	753.82

Full Analysis

In(VOR) + Prop. Grassland + Stocking Density	4	743.56	0.00	0.90	735.55
In(VOR) + Prop. Grassland	3	748.94	5.38	0.06	742.94
In(VOR) + Prop. Grassland + Grazing System + Year	7	749.82	6.26	0.04	735.79
Stocking Density	2	755.05	11.49	0.00	751.05
Grazing System + Year	5	757.17	13.61	0.00	747.15
Null	1	758.94	15.38	0.00	756.94

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

Model	K	AIC _c	ΔAIC _c	AIC _c w_i	Deviance
Null	1	251.86	0.00	0.61	249.85
Stocking Rate	2	253.72	1.86	0.24	249.70
Treatment	3	255.42	3.57	0.10	249.40
Treatment + Stocking Rate	4	257.43	5.58	0.04	249.39
Treatment x Stocking Rate	6	261.46	9.61	0.01	249.39

Table 5. Support for models evaluating effects of management variables on visual obstruction (VOR) at the nest bowl and averaged across the 6 m radius vegetation plot. The number of parameters (K), AIC_c values, ΔAIC_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
<u>Nest VOR</u>						
Stocking Rate	3	1284.35	0.00	0.45	0.45	-639.14
Grazing System + Stocking Rate	5	1285.41	1.06	0.26	0.71	-637.62
Null	2	1286.39	2.04	0.16	0.88	-641.18
Grazing System * Stocking Rate	7	1288.00	3.65	0.07	0.95	-636.85
Grazing System	4	1288.68	4.33	0.05	1.00	-640.29
<u>Average VOR</u>						
Grazing System + Stocking Rate	5	1079.45	0.00	0.49	0.49	-534.64
Grazing System * Stocking Rate	7	1079.80	0.35	0.41	0.90	-532.75
Stocking Rate	3	1082.94	3.49	0.09	0.99	-538.44
Grazing System	4	1087.77	8.32	0.01	1.00	-539.83
Null	2	1089.02	9.57	0.00	1.00	-542.49

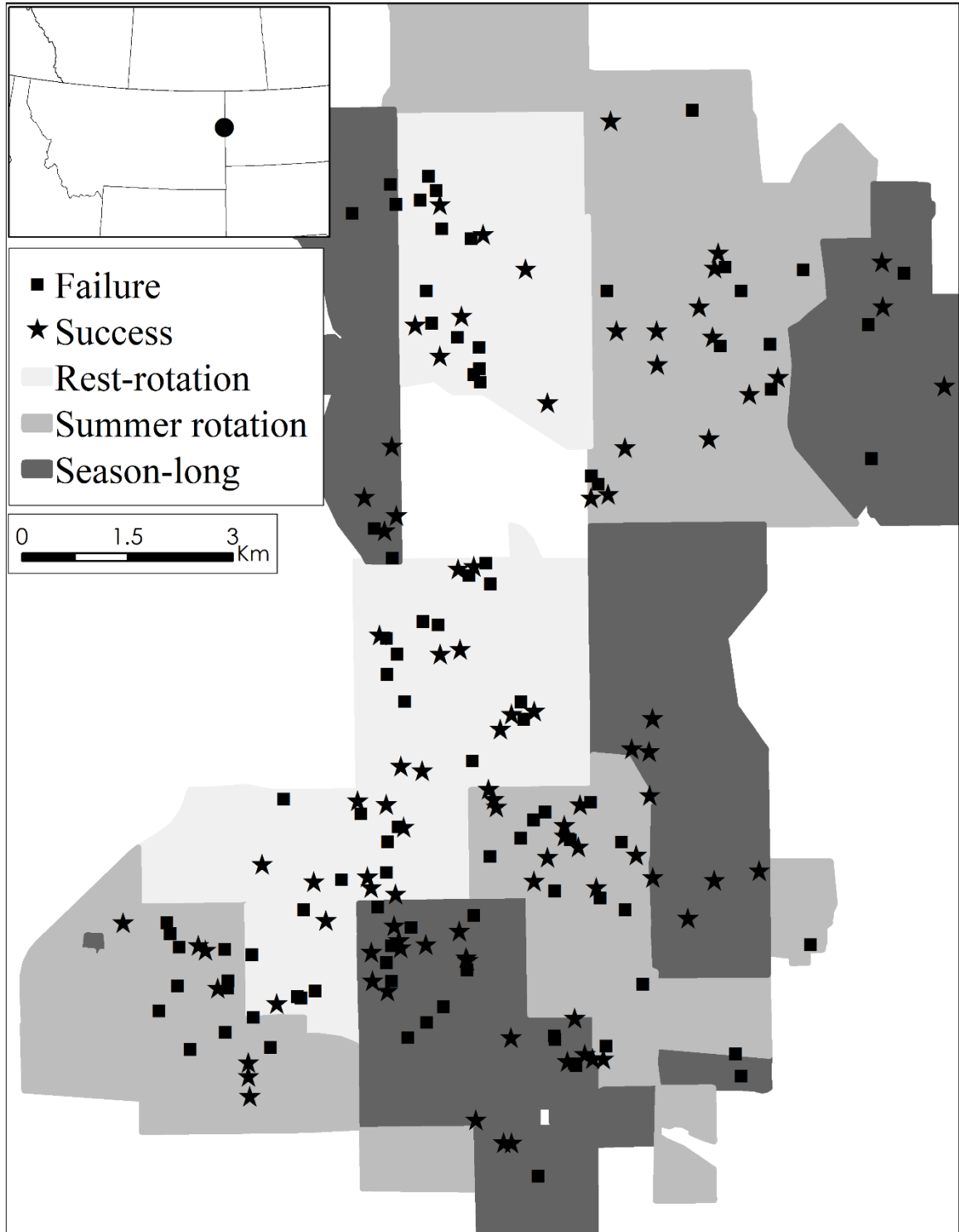


Figure 1. Locations of failed and successful sharp-tailed grouse nests monitored in 2016–18 in relation to different grazing systems.

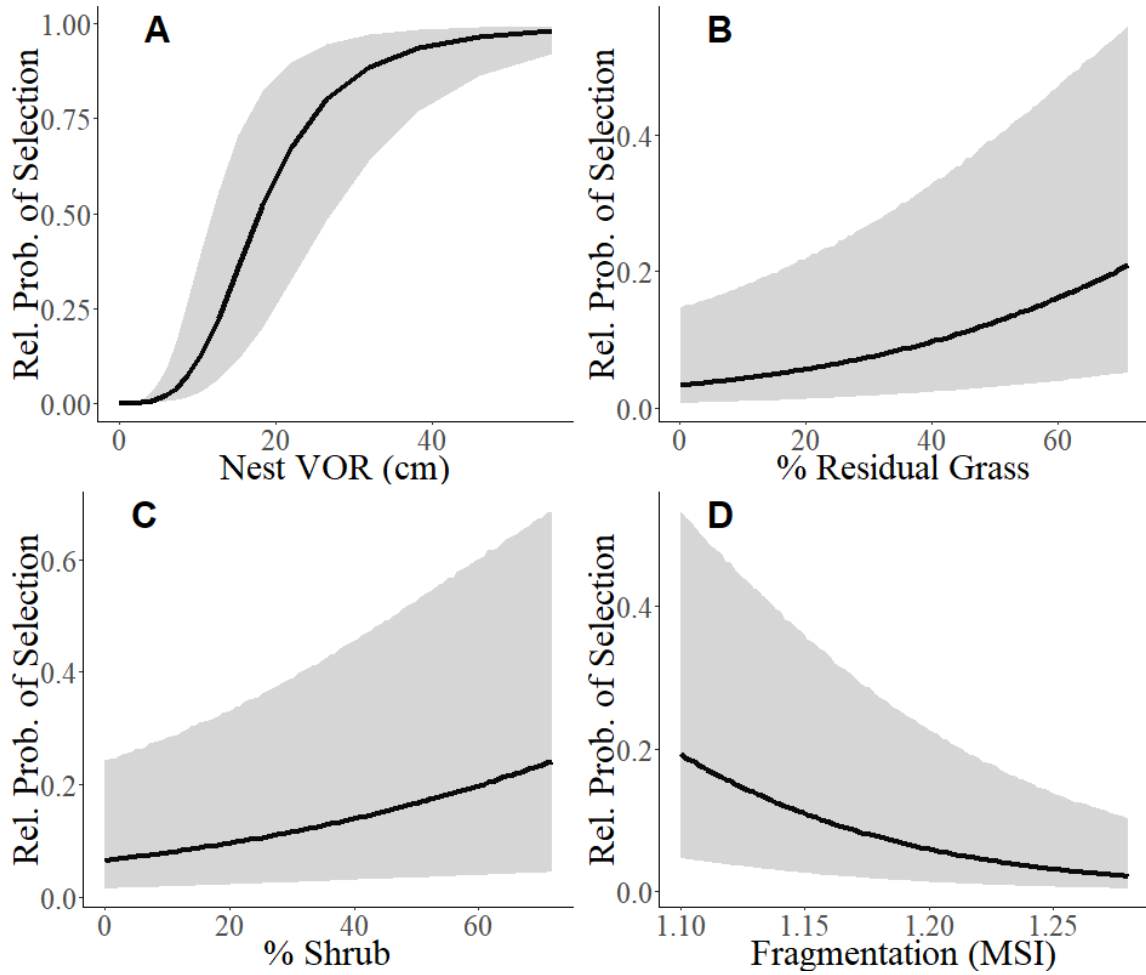


Figure 2. Estimated relative probability of nest site selection in relation to important habitat variables, with 85% confidence intervals shown in grey. Visual obstruction (VOR) was measured at the nest bowl.

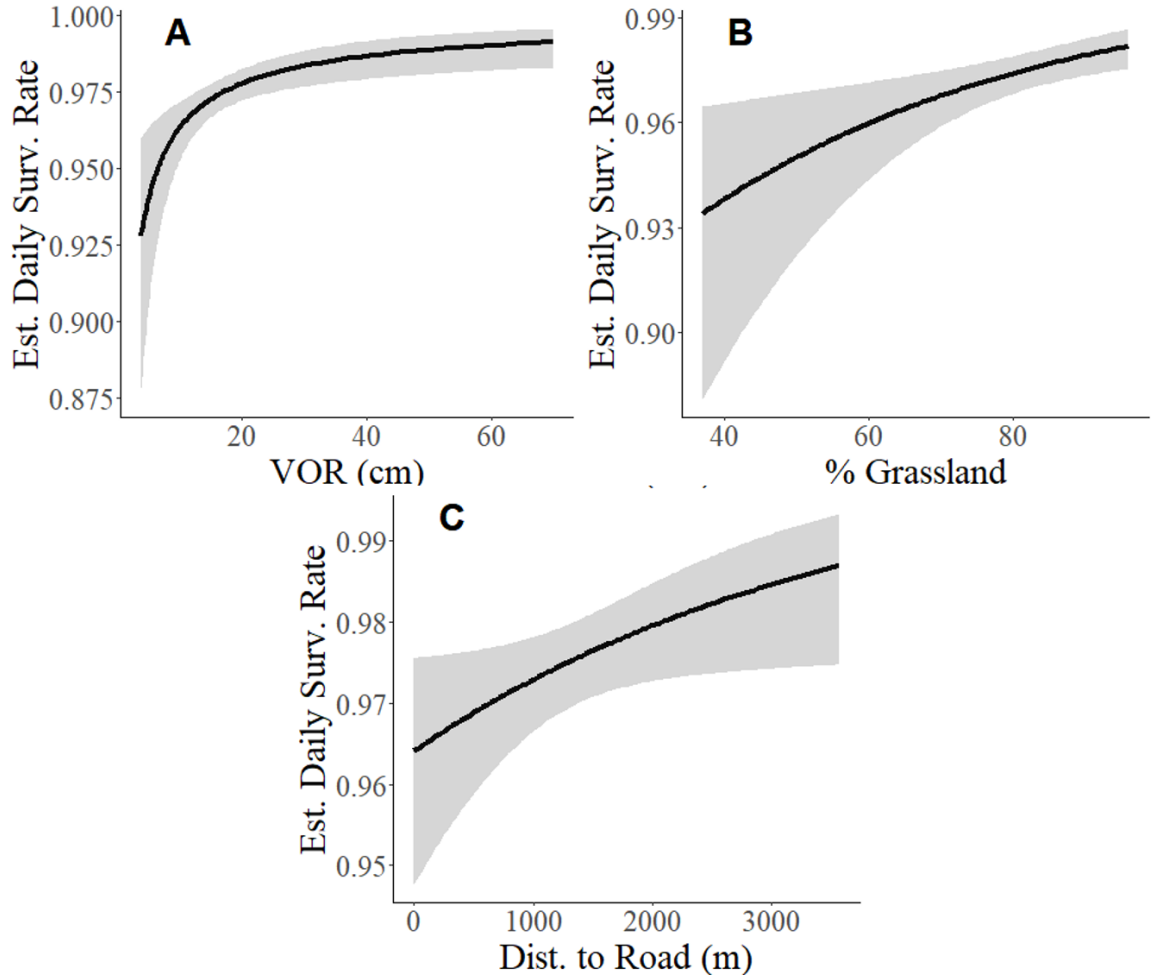


Figure 3. Estimated daily nest survival in relation to important habitat variables, with 85% confidence intervals shown in grey. Visual obstruction (VOR) was averaged across the 6 m vegetation plot.

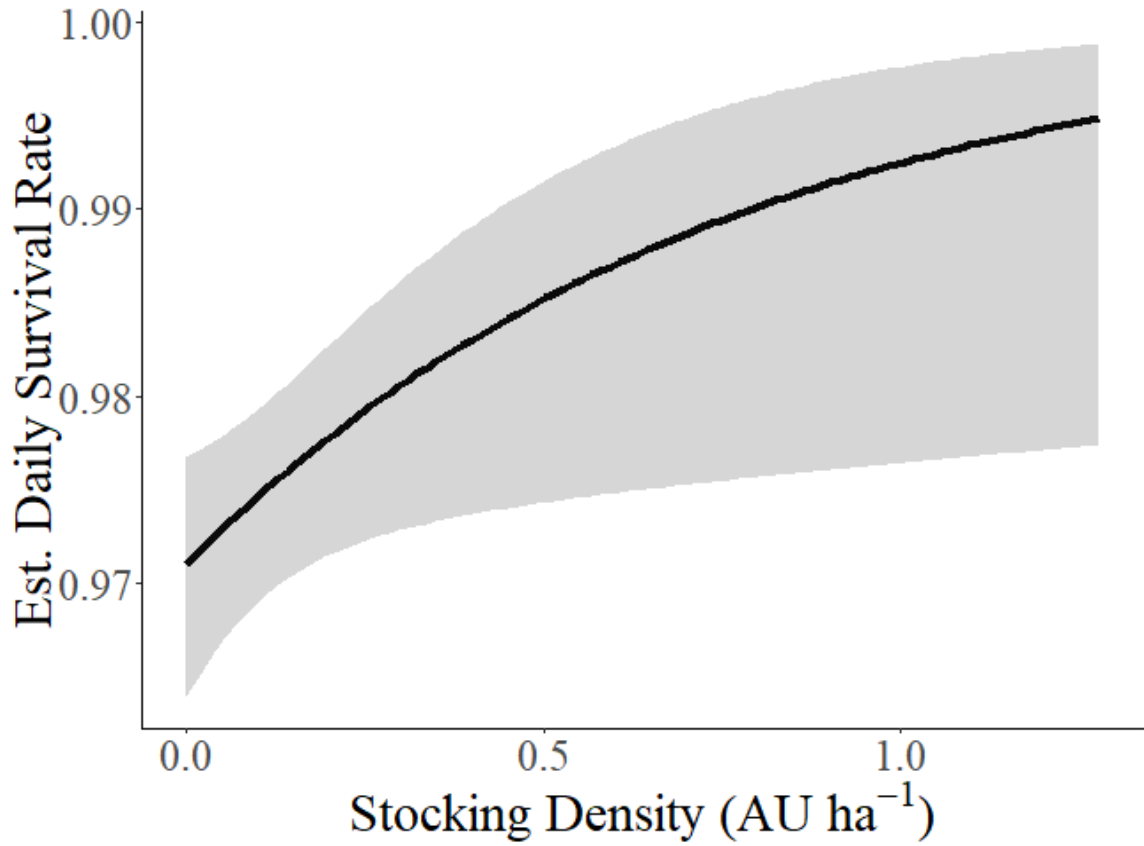


Figure 4. Estimated daily nest survival in relation to stocking density while the nest was active, with 85% confidence intervals shown in grey.

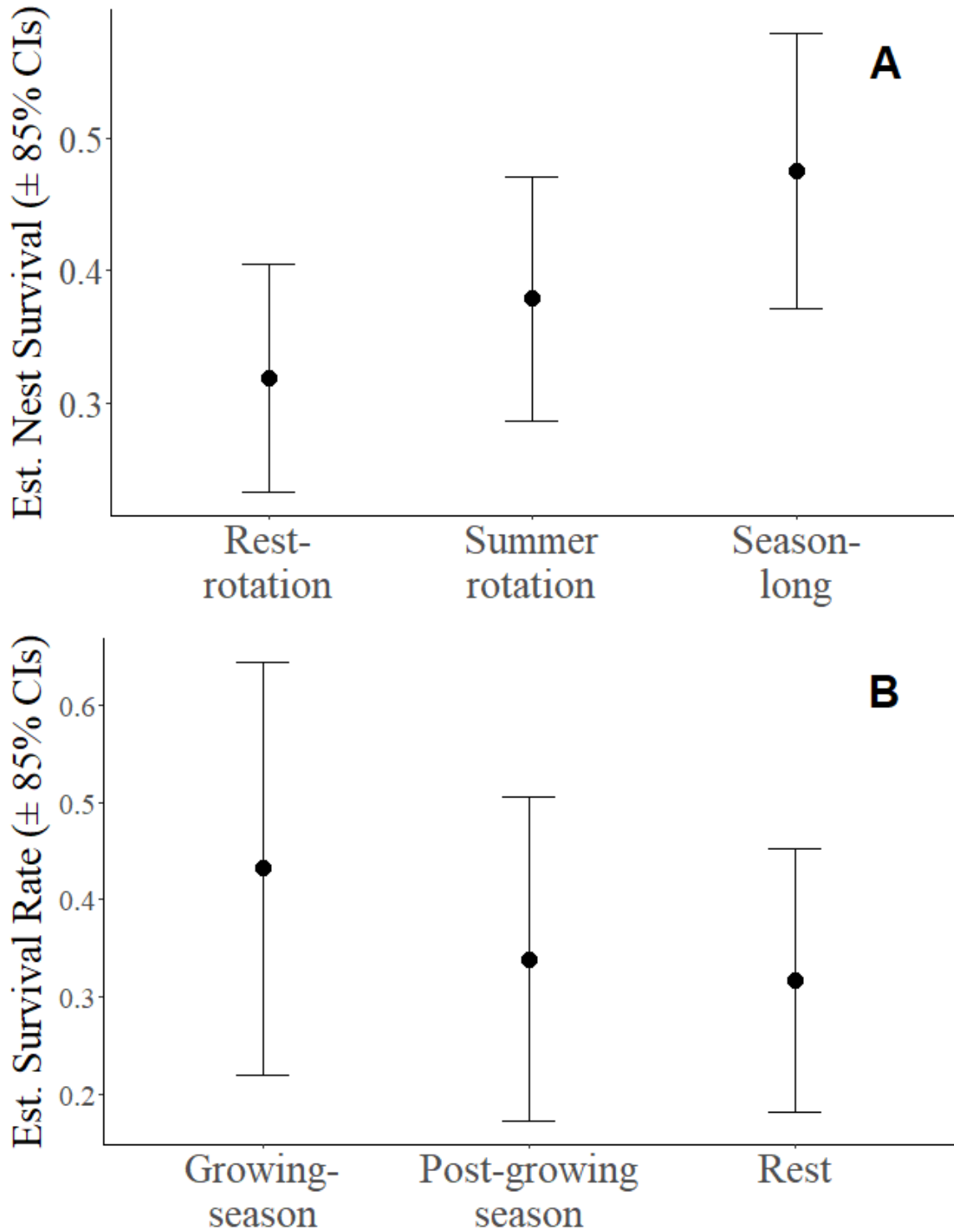


Figure 5. Estimated overall nest survival (\pm 85% confidence intervals) for sharp-tailed grouse in each of the three grazing treatments (A) and in each of the three treatments within the rest-rotation system in 2016–18 (B).

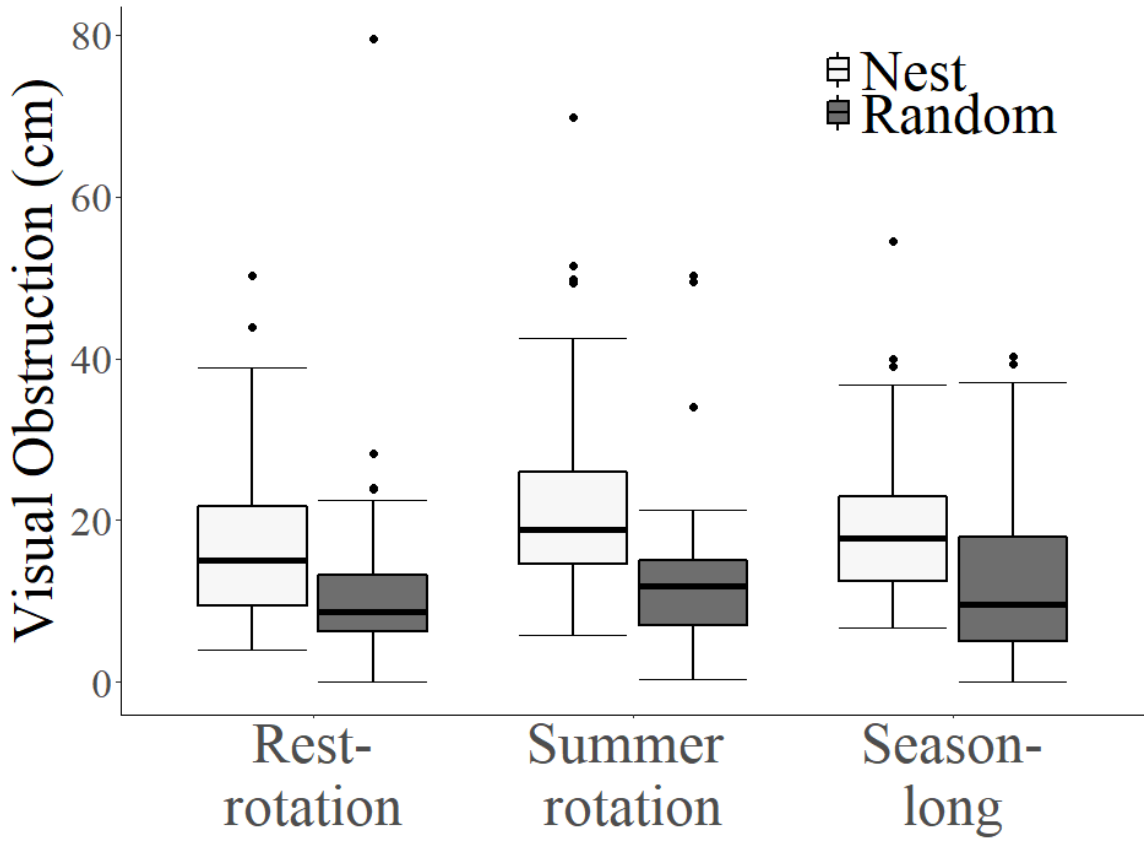


Figure 6. Measured visual obstruction (VOR) within the three grazing systems.

CHAPTER THREE

EFFECTS OF RANGELAND MANAGEMENT ON THE SURVIVAL OF ADULT
SHARP-TAILED GROUSE

Contribution of Authors and Co-Authors

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CHAPTER THREE

EFFECTS OF RANGELAND MANAGEMENT ON THE SURVIVAL OF ADULT
SHARP-TAILED GROUSE

The relationships between habitat selection and population-level responses can have implications for wildlife management and conservation (Donovan and Thompson 2001, Aldridge and Boyce 2007, Frederiksen et al. 2014, Sandercock et al. 2015). Predation is a key force influencing both survival and reproduction and it can shape the life histories of many species which face a trade-off between minimizing predation risk and acquiring resources (Verdolin 2006, Cresswell 2008, Dinkins et al. 2014b). Both resource availability and predation risk vary across the landscape and individuals should balance these competing needs through the process of habitat selection (Verdolin 2006, Aldridge and Boyce 2007, Cresswell 2008). Linking habitat selection to demography is therefore important, because effective conservation requires a thorough understanding of the local and landscape effects on vital rates in order to prioritize appropriate habitats (Aldridge and Boyce 2007, Frederiksen et al. 2014, Sandercock et al. 2015).

Land management has the potential to alter habitat structure and potentially mediate predation risk within and across landscapes. Livestock grazing is the most widespread land management practice in the world (Fleischner 1994, Krausman et al. 2009, Alkemade et al. 2013), and can have a significant impact on wildlife habitat by directly affecting ecosystem composition, function, structure, and productivity (Fleischner 1994, Boyd et al. 2014). Overgrazing has been implicated in the decline of many wildlife populations (Fleischner 1994), but grazing can benefit wildlife if managed

appropriately, particularly by emphasizing heterogeneity-based management practices that provide a variety of resources required to meet seasonal life-history needs (Fuhlendorf and Engle 2001, Derner et al. 2009). Thus, grazing could be a useful management tool to diversify habitats and provide a mosaic of patches in different stages of recovery from disturbance by livestock, which could allow wildlife to balance the need for resources with the risk of predation (Ryder 1980, Fuhlendorf and Engle 2001, Coppedge et al. 2008, Krausman et al. 2009). However, in order for management to meet conservation goals, a mechanistic understanding of the effects of management on habitat-specific demographic performance is required (Sandercock et al. 2015)

Prairie-grouse (*Tympanuchus* spp.) are recognized as indicator species for grassland habitats (Poiani et al. 2001, Roersma 2001). Habitat requirements of prairie-grouse encompass a broad range of vegetational structures, with short, bare areas used for lekking; denser, herbaceous cover for nesting; and thicker shrubs for winter cover and food (Marks and Marks 1988, Derner et al. 2009). As a result, identifying appropriate grazing management strategies to conserve grouse populations could have implications for a suite of grassland species (Hillman and Jackson 1973, Poiani et al. 2001, Roersma 2001). Predation accounts for the majority of prairie-grouse mortality and increased habitat heterogeneity in the form of greater structural and compositional variation in herbaceous vegetation is thought to benefit grouse, although any advantages depend on the scale at which the heterogeneity is relevant to the grouse (Bergerud and Gratson 1988b, Schroeder and Baydack 2001). In the tallgrass prairie, patch-burn grazing is employed as a heterogeneous management technique to create a large-scale patchwork of

grassland habitats, which both increased adult survival of greater prairie-chickens (*T. cupido*) and moderated seasonal patterns of mortality risk (Winder et al. 2018).

Rotational grazing systems, such as the Hormay rest-rotation system, could function similarly to create habitat heterogeneity at the pasture-level in order to meet the range of prairie-grouse habitat requirements (Hormay and Evanko 1958). The rest-rotation system is based on the idea that grazing during consecutive growing seasons can decrease the abundance of desirable grasses and overall range productivity (Hormay and Evanko 1958, Hormay 1970). Stock are therefore moved between pastures so that individual range units are not grazed at the same time each year and a rest period is incorporated to allow for vegetation to periodically complete its growth period without defoliation (Jefferies 1970). In contrast, summer rotation and season-long systems graze pastures at the same time each year and each pasture is grazed every year, such that an entire year of rest is not incorporated. While originally developed to improve range condition, rest-rotation could conceptually create pasture-level heterogeneity with a range of habitat conditions including increased residual cover in pastures that were rested the previous year (Frisina 1991, Montana Department of Fish, Wildlife & Parks 2011). Alternatively, grazing management could influence the predator community by altering either prey abundance or predator foraging efficiency (Fuller and Sievert 2001). By producing pasture-level heterogeneity, the rest-rotation system could create more even forage utilization and lower within-pasture heterogeneity in vegetation structure, thus resulting in improved foraging efficiency of mesocarnivores (Johnson and Temple 1990, Sutter and Ritchison 2005, Vold 2018).

Effects of grazing systems can, however, be mediated by stocking rate, with high stocking rates shown to have significant negative effects on multiple aspects of prairie-grouse demography (McNew et al. 2015, Kraft 2016, Winder et al. 2018). Rangeland management strategies can also interact with weather and climatic conditions, with potential benefits reduced in drought years (McNew et al. 2015). Furthermore, adult survival is influenced by local habitat factors and human land use practices. At a large spatial scale, survival of female sharp-tailed grouse (*T. phasianellus*) and lesser prairie-chickens (*T. pallidicinctus*) decreased in landscapes composed of more cropland (Manzer 2004, Robinson 2018), which can fragment grassland habitats and support higher densities of generalist predators (Andr n 1995, Kurki et al. 1998, Winter et al. 2000). Grouse survival is also typically negatively related to energy development and the corresponding increase in roads, fences and powerlines (Holloran et al. 2010, Dinkins et al. 2014a, Hovick et al. 2014b, Robinson 2018). However, one study found an increase in greater prairie-chicken survival following the construction of a wind energy site, possibly mediated by the effect of the development on the local predator community (Winder et al. 2014a).

Our objectives were to evaluate the effects of grazing management on the breeding season survival and habitat-associated mortality risk of adult female sharp-tailed grouse. Grazing systems, such as rest-rotation, that alter the timing of grazing from year to year and periodically rest portions of the landscape, could conceptually create a mosaic of pasture-scale heterogeneity that could benefit wildlife (Frisina 1991, Montana Department of Fish, Wildlife & Parks 2011). Therefore, we compared rest-rotation

grazing to commonly employed systems of summer rotation and season-long and we hypothesized that breeding season survival rates of adult females would be higher in the rest-rotation system, potentially due to increased vegetation heterogeneity. We also hypothesized that mortality risk would be lower in rest-rotation pastures and pastures with lower stocking rates due to higher vegetation heterogeneity.

STUDY AREA

We conducted our study during 2016–2018 in southern Richland and McKenzie Counties in eastern Montana and western North Dakota, respectively (Fig. 7). The study area was composed of Great Plains mixed-grass prairie interspersed with Great Plains badlands and wooded draws and ravines and was primarily managed for cattle production (LANDFIRE 2013). Vegetation was a mixture of mid and short grasses, with western wheatgrass (*Pascopyrum smithii*), little bluestem (*Schizachyrium scoparium*), needle-and-thread (*Hesperostipa comata*), Kentucky bluegrass (*Poa pratensis*), blue grama (*Bouteloua gracilis*), and crested wheatgrass (*Agropyron cristatum*) being the dominant graminoids. Based on both point-count surveys and camera-trap data collected during 2016–2017, potential predators in our study area during the time of this study included coyote (*Canis latrans*), American badger (*Taxidea taxus*), short-tailed weasel (*Mustela ermine*), peregrine falcon (*Falco peregrinus*), prairie falcon (*Falco mexicanus*), northern harrier (*Circus cyaneus*), red-tailed hawk (*Buteo jamaicensis*), golden eagle, (*Aquila chrysaetos*), and great horned owl (*Bubo virginianus*; Vold 2018). Precipitation during the entire year and during the sharp-tailed grouse breeding season differed significantly across the three study years. We calculated the amount of precipitation received during

the year (1 January–31 December) and the breeding season (15 March–15 August) using daily precipitation data from the National Oceanic and Atmospheric Association (NOAA) station in Sidney, MT. Total annual precipitation was 419.3 mm in 2016, 216.4 mm in 2017, and 341.5 mm in 2018. Total breeding season precipitation was 268.7 mm in 2016, 105.2 mm in 2017, and 312.1 mm in 2018.

The study area included an ~3,300-ha Upland Gamebird Enhancement Program (UGBEP) project established by the Montana Department of Fish, Wildlife and Parks in 1993 (Montana Department of Fish, Wildlife & Parks 2011) that included four separate but contiguous 3-pasture Hormay rest-rotation systems (Hormay and Evanko 1958). In the first year, cattle were stocked in one pasture from May–July (growing season), then moved to a second pasture during August–October (post-growing season), while the third pasture was rested for the entire year. The order of rotation was shifted within each 3-pasture rest-rotation system the next year so that no pasture was grazed during the same season in consecutive years and pastures rested in the previous year theoretically should have the most residual cover. Average pasture size in the rest-rotation system was 292 ± 116 ha. Pastures of surrounding ranches, which included both private land and 4 pastures located on U.S. Forest Service National Grasslands were managed with more commonly used livestock grazing systems, including both season-long systems (19 pastures, ~4,800 ha) and 2- and 3-pasture summer rotation systems (25 pastures, ~5,200 ha). Grazing occurred in season-long pastures from approximately May to early November, while cattle were stocked in the same pastures in summer rotation systems each year for the same 6–8-week period (approximately April–June, June–July or Aug–Nov). Average

pasture sizes in the season-long and summer rotation systems were 242 ± 312 ha and 238 ± 335 ha, respectively. Pastures were stocked primarily with cow-calf pairs and stocking rates were controlled by landowners and lessees. Averaged rates at a pasture-level were 0.93 AUM ha⁻¹, 1.46 AUM ha⁻¹, and 0.76 AUM ha⁻¹ for rest-rotation, season-long, and summer rotation pastures, respectively. The range of stocking rates for grazed pastures was $0.38 - 3.25$ AUM ha⁻¹, $0.17 - 4.28$ AUM ha⁻¹, and $0.21 - 4.45$ AUM ha⁻¹ for rest-rotation, season-long, and summer rotation pastures, respectively, and included similar distributions within each grazing system (Milligan et al., In press). Average stocking rates were below or within the range of rates ($1.11 - 1.48$ AUM ha⁻¹) recommended by the Natural Resources Conservation Service (NRCS) for the most common ecological site (R058AE001MT) in the study area. Environmental variables, including topography, average vegetation productivity, soil type, vegetation canopy greenness as measured by the Normalized Vegetation Index (NDVI) in June 2018, and the variation in small-scale vegetation cover and structure were similar among grazing systems (Table 6; Milligan et al., In press).

METHODS

We captured grouse using walk-in funnel traps at 12 leks (5 in rest-rotation pastures, 3 in summer rotation pastures, and 4 in season-long pastures) during March–May. Females were fitted with very high frequency (VHF) radio-transmitters (model A4050; Advanced Telemetry Systems, Isanti, MN). Radio-marked females were located by triangulation or homing ≥ 3 times/week during the breeding season (15 March–15 August) and 1 time per month during the non-breeding season (September–March). The breeding season was

defined as extending from the beginning of lekking in the spring to the end of brood break-up in the fall. Transmitters were equipped with a mortality switch that activated after 6–8 hours of inactivity. Once the mortality switch activated, transmitters were located, Global Positioning System (GPS) locations of presumed mortalities were recorded, and the area searched to determine probable cause of death. Mortality events were classified as either predation, hunter, or unknown. Females were censored from the study if their collars were found with no sign of death or if they could not be located for \geq 2 months. We did not separate predation events based on cause-specific mortality due to the confounding effects of scavenging activity (Milligan and McNew, In press). All animal handling was approved under Montana State University's Institutional Animal Care and Use Committee (Protocol #2016-01).

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. We then calculated the following grazing management variables: grazing system (rest-rotation, summer rotation, season-long) and stocking rate (AUM ha⁻¹), which is a measure of the number of animals in a pasture during the entire grazing season, during both the current and previous year.

Statistical Analyses

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

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

We calculated cumulative survival rates of radio-marked females for the 7-month non-breeding season separately using staggered entry Kaplan-Meier models with monthly

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

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

Seasonal mortality risk.— 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 (DeGiudice 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.

Spatial correlates 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 form 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 ($r \geq 0.5$; Appendix D).

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 AIC_c and based model selection on both the minimization of AIC_c ($\Delta\text{AIC}_c < 2$ from best-fit model) and AIC_c weights ($\sum w_i > 0.3$). Models that differed from the top model by a single parameter with $\Delta\text{AIC}_c < 2.0$ or whose 85% confidence intervals overlapped zero were considered uninformative (Arnold 2010).

RESULTS

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%).

Breeding and non-breeding seasonal survival.— The assumption of proportional hazards for breeding season survival was not met for either year or grazing system, so models that included those variables also incorporated an interaction with time. Overall survival (\pm SE) during the 5-month breeding season for female sharp-tailed grouse across all years and grazing systems was 0.65 ± 0.04 , which corresponds to a monthly survival rate of 0.91 ± 0.005 . Despite significant annual variation in precipitation, breeding season

survival did not differ significantly among the 3 years of study (baseline: 2016; Cox proportional HR for 2017 = 0.72, 95% CI = 0.07–7.02, $Z = -0.29$, $P = 0.78$; Cox proportional hazards HR for 2018 = 5.7, 95% CI = 0.52–63.74, $Z = 1.42$, $P = 0.16$). There was also no difference in breeding season survival between female age classes (baseline: second-year; Cox proportional hazards HR = 1.19, 95% CI = 0.72–1.96, $Z = 0.69$, $P = 0.49$), or among grazing systems (baseline: season-long; Cox proportional hazards HR for summer-rotation = 1.13, 95% CI = 0.15–8.82, $Z = 0.12$, $P = 0.90$; Cox proportional hazards HR for rest-rotation = 1.49, 95% CI = 0.17–13.29, $Z = 0.36$, $P = 0.73$). Although there was weak evidence for an effect of age and year on survival (Table 7), confidence intervals for both age groups (second-year: 0.524–0.735, after second-year: 0.558–0.757) and all 3 years (2016: 0.540–0.793, 2017: 0.540–0.778, 2018: 0.545–0.785) entirely overlapped. Breeding season survival was similar across grazing systems (Fig. 8).

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.

Seasonal mortality risk.— 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. 9), 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. 9). 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. 9). 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. 8).

Spatial correlates of mortality risk.— 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

(Appendix D). 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 (Appendix D) and so were included in the full candidate model set with grazing management variables. There was no evidence for an effect of anthropogenic disturbance, including either oil pads or roads. In the full model set, the top model contained the effect of cropland within 1,300 m, which accounted for 49% of the relative support of the data across all models (Table 8). The risk score increased with the amount of cropland within 1,300 m of a bird's location ($\beta = 0.02 \pm 0.02$; Fig. 10). 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).

DISCUSSION

Monthly survival was lower during the breeding season in 2 of 3 study years, which is consistent with previous studies of grouse (Hannon et al. 2003, Manzer and Hannon 2008, Blomberg et al. 2013, Winder et al. 2018). Breeding season survival was consistent across years, despite significant variation in precipitation during the study period, whereas non-breeding season survival and annual survival were significantly lower in 2017, which corresponded to a severe drought. However, we found no evidence that grazing management, including either grazing system or stocking rate, influenced breeding season survival or habitat-associated mortality risk. There was a difference in the seasonal patterns of mortality risk among grazing systems that may represent a trade-

off in mortality risk but did not influence cumulative breeding season survival. However, the amount of cropland at a broad scale influenced mortality risk, with risk being higher in landscapes with a greater proportion of cropland.

Our estimates of both breeding season (0.65) and annual survival (0.28-0.50) were within the range of estimates previously reported for prairie-grouse (Hagen et al. 2007: 0.30-0.59, Manzer and Hannon 2008: 0.43, Williamson 2009: 0.43-0.72, McNew et al. 2012: 0.34-0.71, Gillette 2014: 0.55-0.63, Winder et al. 2014a: 0.32-0.57), although sharp-tailed grouse have received less research attention than related species. Breeding season survival estimates in our study were higher than those reported in a study in Alberta (0.53), although annual estimates were similar to both that study and another study in North Dakota (Manzer and Hannon 2008, Williamson 2009). Our estimates of both adult survival and productivity were in line with those from a study in Idaho where demographic population models indicated a stable population (Gillette 2014, Milligan et al., In press). Furthermore, annual lek count data collected concurrently with our study suggest a fluctuating but stable population of sharp-tailed grouse at our study area.

We evaluated multiple aspects of grazing management and found no evidence for an effect on adult breeding season survival, which is inconsistent with findings of previous studies of other prairie-grouse populations (Kraft 2016, Winder et al. 2018). The heterogeneity-focused management system of patch-burn grazing had significant benefits for the survival of greater prairie-chickens in the tallgrass prairies of Kansas (Winder et al. 2018), but the rest-rotation grazing system, which could conceptually create similar pasture-level heterogeneity, was not increasing variation in vegetation cover at our study

site in eastern Montana (Table 6; Milligan et al., In press). The survival of lesser prairie-chickens in Oklahoma was related to microhabitat characteristics and was associated with higher density of both shrubs and grasses (Patten et al. 2005). Our research suggests that grazing system was not an important driver of variation in small-scale vegetation cover during the nesting period (Table 6; Milligan et al., In press), which could explain the lack of an effect of grazing system if adult survival was linked to small-scale vegetation variables. Furthermore, there was no evidence for an effect of stocking rate, either from the current or the previous year, on adult survival, whereas higher stocking rates and the related measure of forage utilization were negatively related to survival of greater sage-grouse (*Centrocercus urophasianus*) and both greater and lesser prairie-chickens (Kraft 2016, Dettenmaier 2018, Winder et al. 2018). However, average stocking rates in our study area were below or within the range recommended by the NRCS; it is possible that grazing system may be an important determinant of mortality risk at higher stocking rates (McNew et al. 2015).

Although we found no evidence for an effect of grazing management on grouse survival, a concurrent study at the same site found higher occupancy of mesocarnivores in the rest-rotation system compared to other grazing systems and higher occupancy in areas with higher stocking rates (Vold 2018). This suggests that grouse survival may not be directly linked to mesocarnivore occupancy if sufficient cover is available so that individuals can select habitat that mediates predation risk. Previous research suggests that mesocarnivore foraging efficiency is lower in rangelands characterized by small-scale within-pasture heterogeneity created by the selective foraging of cattle or inherent

edaphic or topographic variability (Johnson and Temple 1990, Bailey et al. 1998, Fuhlendorf and Engle 2001, Sutter and Ritchison 2005), which is more consistent with vegetation patterns in our study area. However, we do not have information on densities of avian predators within each of the three grazing systems, which may be related to grouse survival or counterbalance effects of mesocarnivores.

While breeding season survival did not differ among grazing systems, patterns of seasonal mortality appeared to vary among the systems. Consistent with previous studies of seasonal mortality risk, there was a peak in mortality during the nesting period across all grazing systems. However, we observed higher mortality risk in the rest-rotation system compared to either season-long or summer rotation, which corresponds to results from our study site that found lower rates of nest survival in the rest-rotation compared to the season-long system (Milligan et al., In press). Furthermore, previous research in our study area found higher rates of mesocarnivore occupancy in the rest-rotation system compared to that found in other grazing systems (Vold 2018), which could translate to greater mortality while females are attending a nest. In contrast, there was a peak in mortality risk towards the end of the breeding season in both season-long and summer rotation systems that was not observed in the rest-rotation systems. Cover is presumably lower later in the grazing season as grazing pressure and utilization accumulate. While we did not observe a difference in vegetation cover among systems earlier during the nesting period (Table 6; Milligan et al., In press), it is possible that there may be differences among grazed and rested or deferred pastures that are more apparent later in the season, although, to our knowledge, no studies have evaluated this relationship. If the

amount or variability of cover does differ between grazed and rested pastures later in the season, females using the rest-rotation system may be able to mitigate predation risk by using the rested or deferred pastures, thus decreasing their mortality risk during that period. Importantly, though, these patterns may represent life history trade-offs regarding survival that are balanced out over time, resulting in no difference in cumulative breeding season survival.

Consistent with previous studies (Ryan et al. 1998, Manzer 2004, Smith et al. 2016, Robinson 2018), grouse survival declined with the amount of cropland at broad spatial scales, with a risk of mortality 1.27 times higher for a female with 10% cropland within 1,300 m of her location compared to a female with no cropland around her location. Similarly, survival of female sharp-tailed grouse was moderately lower in areas with more cropland within 1,600 m (Manzer 2004) and populations of greater sage-grouse were sensitive to even small increases in the amount of cropland across broad spatial extents (Smith et al. 2016). Predation was the major cause of mortality in our study and landscapes with greater proportions of cropland could sustain larger populations of generalist predators such as coyotes (Kurki et al. 1998). Mesocarnivores, primary predators of sharp-tailed grouse, also often exhibit positive responses to fragmentation (Andr n 1995, Winter et al. 2000), which could explain decreases in survival with more cropland on the landscape.

MANAGEMENT IMPLICATIONS

Globally, livestock grazing is a dominant land use that could impact demography by influencing habitat structure and thus predation risk across the landscape. Understanding the relationship between demography and land management and related habitat variables is necessary for effective wildlife conservation (Aldridge and Boyce 2007, Frederiksen et al. 2014, Sandercock et al. 2015). Heterogeneity-based management has had benefits for grassland wildlife in the more mesic tallgrass prairie (Fuhlendorf and Engle 2004, McNew et al. 2015, Winder et al. 2018) and rest-rotation grazing could conceptually create a similar mosaic of habitat by altering the timing of grazing and providing periods of rest (Frisina 1991, Montana Department of Fish, Wildlife & Parks 2011). However, our results indicate that rest-rotation grazing did not create measurable differences in the cumulative survival of adult female sharp-tailed grouse, potentially because the grazing system did not increase vegetation heterogeneity at a spatial scale relevant to the mortality risk of grouse. Our study area was also naturally heterogeneous, both edaphically and topographically, which could outweigh any effects of grazing system on heterogeneity. Furthermore, stocking rates were moderate across the study area, so it is possible that an effect may be observed in regions with higher stocking rates or less inherent landscape variability.

Our results suggest that management approaches, such as specialized grazing systems, may not influence the survival of sharp-tailed grouse in the northern mixed-grass prairie where stocking rates of livestock are moderate. Furthermore, cropland conversion represents the largest threat to grassland wildlife (Hoekstra et al. 2005,

Stephens et al. 2008, Robinson 2018), and we found evidence for a negative effect of cropland on the mortality risk of sharp-tailed grouse. Therefore, ranching strategies that preserve unfragmented grassland habitats on the landscape may have the largest benefits for sharp-tailed grouse survival. Nevertheless, our estimates of survival are consistent with previous studies on stable populations (Gillette 2014), suggesting that survival rates are not likely an issue of concern for management in eastern Montana and western North Dakota at this time.

Table 6. Coefficient of variation for vegetation measurements in each grazing system. Reported p-values are from the Feltz and Miller (1996) asymptotic test for the equality of coefficients of variation.

	Rest-rotation	Summer rotation	Season-long	p-value
VOR	89.56	77.09	85.56	0.76
% Grass	47.74	49.82	41.61	0.52
% Residual grass	56.82	57.50	66.73	0.55
% Forb	75.64	100.47	68.97	0.14
% Shrub	137.20	197.01	224.83	0.33
% Bare	78.25	93.92	97.18	0.50

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

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

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

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. w_i	LL
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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

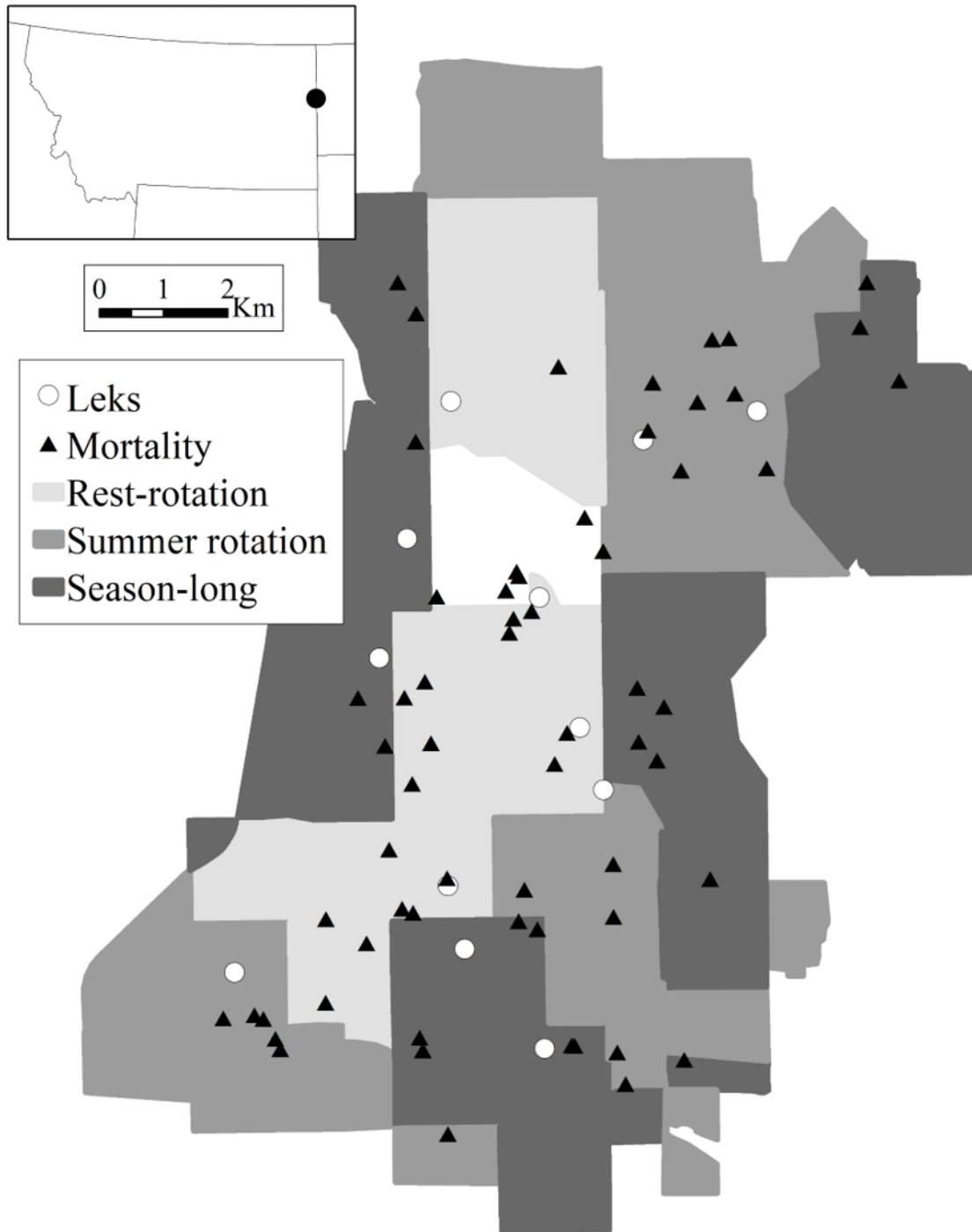


Figure 7. Study area in eastern Montana and western North Dakota with the 3 grazing systems shown in gray, capture leks represented by white circles, and female mortality locations represented by black triangles.

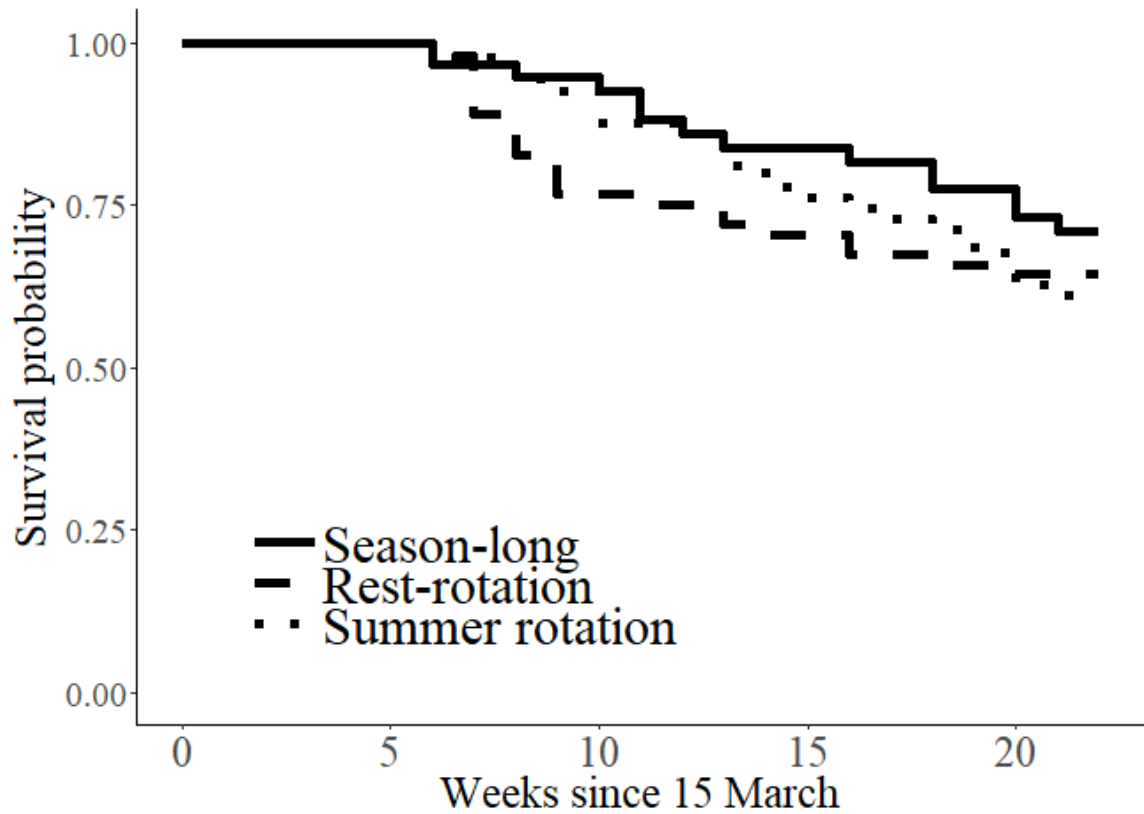


Figure 8. Kaplan-Meier plot of cumulative weekly survival during the breeding season of radio-marked female sharp-tailed grouse associated with 3 grazing systems in eastern Montana and western North Dakota. Confidence intervals omitted for clarity.

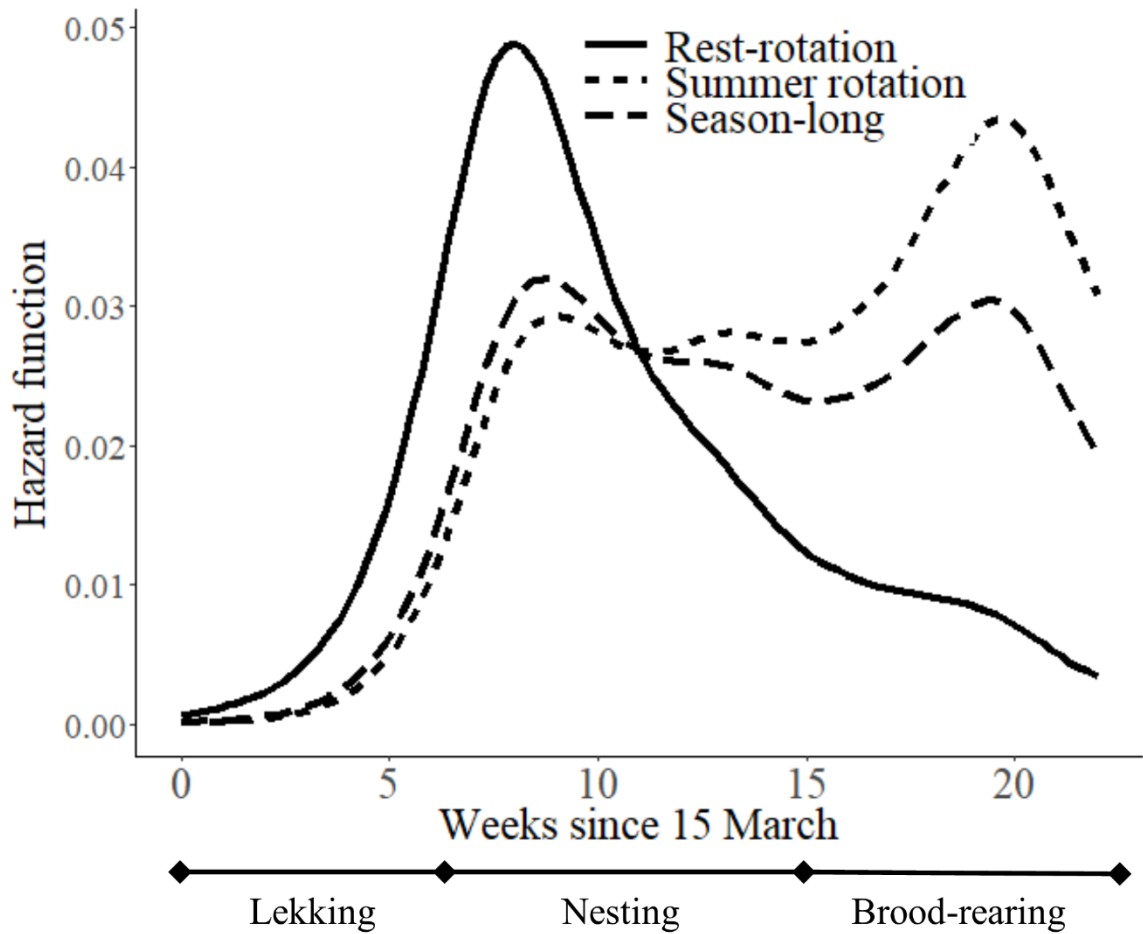


Figure 9. Weekly hazard functions during the breeding season for female sharp-tailed grouse associated with 3 grazing systems in eastern Montana and western North Dakota. Confidence intervals omitted for clarity. The approximate timing of lekking, nesting, and brood-rearing activity is shown at the bottom.

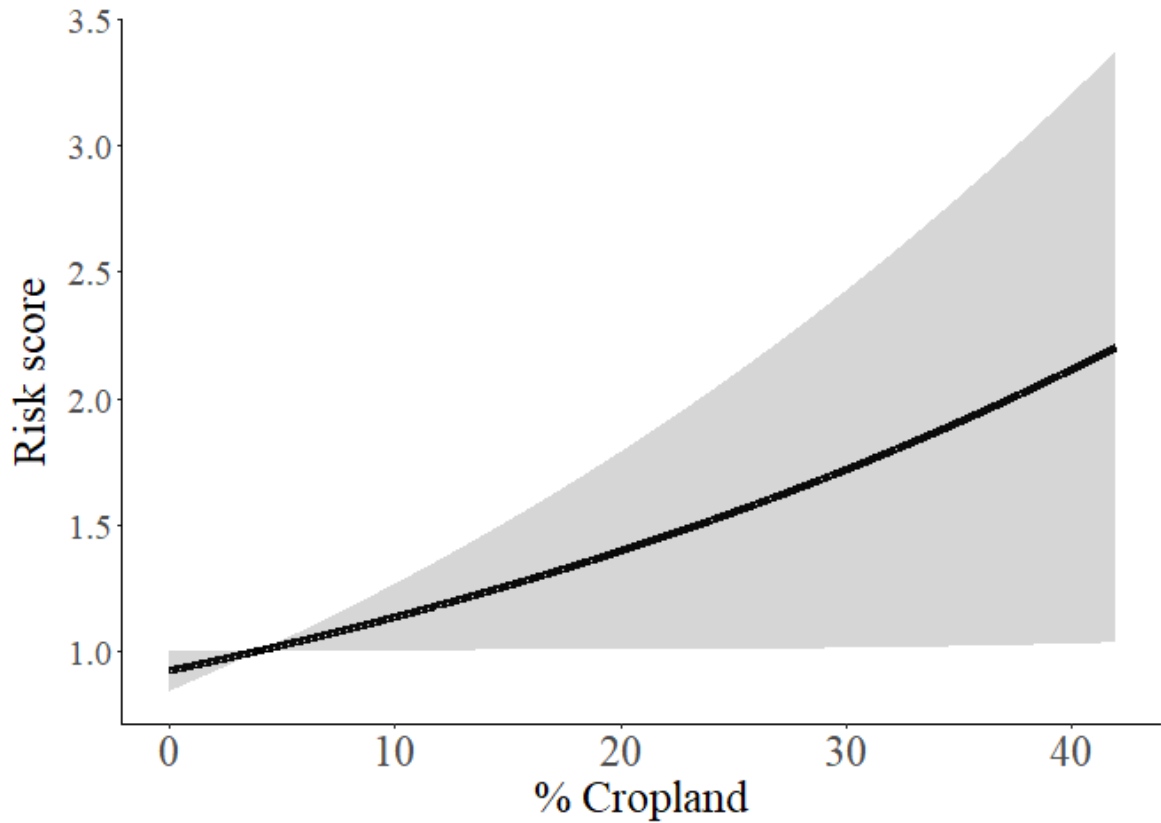


Figure 10. Risk score (\pm 85% confidence intervals) from an Andersen-Gill formulation of the Cox proportional hazards model estimating the risk of mortality for female sharp-tailed grouse relative to the percent cropland within 1,300 m in eastern Montana and western North Dakota.

CHAPTER FOUR

EFFECTS OF RANGELAND MANAGEMENT ON THE HABITAT SELECTION OF
SHARP-TAILED GROUSE IN THE MIXED-GRASS PRAIRIE

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Manuscript in Chapter 4

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CHAPTER FOUR

EFFECTS OF RANGELAND MANAGEMENT ON THE HABITAT SELECTION OF
SHARP-TAILED GROUSE IN THE MIXED-GRASS PRAIRIE

Habitat selection, especially for reproduction, is an important individual decision-making process that links individual behavior to population abundance and determines the spatial distribution of both species and individuals (Jones 2001, Johnson 2007, Boyce et al. 2016). The process of habitat selection represents a trade-off in which individuals balance competing demands such as acquiring resources and avoiding predators to maximize fitness (Beyer et al. 2010, McLoughlin et al. 2010). Thus, habitat selection is a key behavior that allows individuals to respond to spatial and temporal variation in their environment (Hebblewhite and Merrill 2009), and research increasingly suggests that both demography and habitat selection of wildlife populations vary spatially (Wiens and Milne 1989, Hagen et al. 2009, McNew et al. 2013, Allen et al. 2014). Effective conservation and management actions therefore need to consider spatial and individual variation in behavior, which can translate to effects at the population level (Leclerc et al. 2016).

Land management has the potential to alter both the structure and composition of habitats and thus can influence the habitat selection of individuals and populations. Livestock grazing is the dominant land use worldwide and can influence the structure, composition, and productivity of habitats (Fleischner 1994, Krausman et al. 2009, Alkemade et al. 2013, Boyd et al. 2014). While overgrazing has been implicated in the decline of many wildlife species (Fleischner 1994), properly managed grazing benefits

populations both by keeping native rangelands on the landscape and by providing a mosaic of habitats in different stages of disturbance, thus mimicking historic disturbance regimes (Fuhlendorf and Engle 2001, Coppedge et al. 2008, Krausman et al. 2009). Specialized grazing systems that focus on creating structural and compositional heterogeneity in vegetation have increased in popularity recently and some management systems, most notably patch-burn grazing in the tallgrass prairie, have been shown to benefit both cattle productivity and a wide variety of wildlife species (Coppedge et al. 2008, Engle et al. 2008, Fuhlendorf et al. 2010, Limb et al. 2011, McNew et al. 2015, Winder et al. 2018). However, the effects of grazing on both wildlife and vegetation vary across broad spatial scales and are often strongly influenced by mediating factors such as precipitation and soil productivity (Holechek et al. 1999, Briske et al. 2008, Krausman et al. 2009, Schieltz and Rubenstein 2016, Lipsey and Naugle 2017).

Rest-rotation grazing is a specialized grazing system that could function similarly to patch-burn grazing (Frisina 1991, Montana Department of Fish, Wildlife & Parks 2011) in areas where fire is not a socially acceptable management technique such as parts of the Great Plains (Sliwinski et al. 2018). Originally developed to improve range condition (Hormay 1970), the Hormay rest-rotation system is based on the idea that grazing during consecutive growing seasons will reduce plant vigor and that rest from grazing is necessary to allow plants to recover (Hormay and Evanko 1958, Hormay 1970). By altering the timing of grazing for individual pastures each year and incorporating an additional period of rest, rest-rotation grazing could also create a patchwork of habitats on the landscape, with rested pastures having the most residual

cover (Frisina 1991, Montana Department of Fish, Wildlife & Parks 2011). By utilizing a patchwork of habitats, individuals may be able to better balance foraging activities with predator avoidance. The effects of grazing system, however, are also influenced by stocking rate, which is a measure of grazing intensity, and long-term high stocking rates can have negative effects, particularly on grouse (Briske et al. 2008, McNew et al. 2015, Kraft 2016, Winder et al. 2018).

Recognized as an indicator species for grassland habitats (Roersma 2001), sharp-tailed grouse (*Tympanuchus phasianellus*) are a model species to evaluate the effects of livestock grazing on wildlife. Prairie grouse (*Tympanuchus* spp.) have diverse habitat requirements throughout their life history, including short, bare areas for lekking, denser herbaceous cover for nesting, and deciduous shrubs for winter cover and food. Identifying management strategies to conserve grouse populations can therefore have implications for a variety of other grassland species (Hillman and Jackson 1973, Poiani et al. 2001). However, very little is known about the general spatial ecology of sharp-tailed grouse and specifically the effects of livestock grazing on their space use.

Habitat selection by grouse is driven in part by predator avoidance, so having sufficient cover is important to conceal both nests and adults (Bergerud and Gratson 1988b). Therefore, grazing, which can influence both the structure and composition of habitats, could have a large effect on grouse selection behavior. Patch-burn grazing, a management strategy that creates heterogeneity in the tallgrass prairie, improved habitat for greater prairie-chickens (*T. cupido*) relative to intensive early stocking, which incorporates stocking rates similar to season-long systems but concentrates grazing

activity during the first half of the growing season, by creating preferred patches in areas with low stocking rates and high fire frequency (Winder et al. 2017). Beyond the effects of patch-burn grazing on prairie-chickens, however, the effects of livestock grazing on prairie grouse are not well understood (Dettenmaier et al. 2017).

Other factors, such as landscape configuration and anthropogenic development, can also influence selection. The surrounding landcover influences grouse habitat selection, with grouse attempting to minimize predation risk at multiple spatial scales by typically selecting for more horizontal and vertical cover (Marks and Marks 1987, Saab and Marks 1992, Goddard et al. 2009), sites with more grassland on the landscape (Ryan et al. 1998, Niemuth 2003, Winder et al. 2015), and less cropland (Cope 1992, Manzer 2004, but see Goddard et al. 2009). Other studies, however, suggest that landcover does not have a large influence on selection or that selection for different habitat types varies among sites (Cope 1992, Winder et al. 2014b, Winder et al. 2015). Anthropogenic development also generally has negative effects on grouse. Greater sage-grouse (*Centrocercus urophasianus*) selected for lower densities of oil and gas development and greater and lesser prairie-chickens (*T. pallidicinctus*) avoided anthropogenic structures, with larger home ranges, typically an indicator of lower habitat quality, in proximity to wind energy development (Hagen et al. 2011, Dinkins et al. 2014b, Winder et al. 2014b). Home range size was not related to road density, however, and selection for or against roads varied among study areas for prairie-chickens (Winder et al. 2015). Further complicating relationships, aspects of habitat selection can change from year to year with different weather conditions (Winder et al. 2017), and can vary across spatial scales, with

home range size for prairie-chickens, for example, related to the amount of precipitation received at different sites spread across multiple states (Winder et al. 2015). Taken together, the lack of information for sharp-tailed grouse and the differing results for related species across time and space make generalized habitat management recommendations inappropriate.

Our objective was to evaluate the grazing management and habitat features associated with sharp-tailed grouse breeding season habitat selection at multiple spatial scales. Habitat selection is a hierarchical process and studies that evaluate selection at multiple spatial scales can improve understanding of wildlife-habitat relationships (Johnson 1980, McDonald et al. 2012). Therefore, we evaluated both second- and third-order habitat selection of female grouse, defined as the selection of habitat for an individual's home range within the larger study area and the selection of habitat within an individual's home range, respectively (Johnson 1980). Livestock grazing has the potential to maintain unfragmented grassland habitats (Curtin et al. 2002) and we hypothesized that grouse would select for relatively unfragmented grassland patches at all scales of selection. Furthermore, rest-rotation grazing could influence grouse habitat selection by creating a patchwork of habitats that are periodically rested from disturbance. Therefore, we hypothesized that if rest-rotation grazing is increasing heterogeneity in grassland habitats, then females would select for rest-rotation pastures and have smaller home ranges when using those potentially higher-quality pastures due to increased availability or proximity of important resources.

STUDY AREA

This study was conducted during 2016–2018 in southern Richland and McKenzie Counties in eastern Montana and western North Dakota, respectively. The study area was composed of Great Plains mixed-grass prairie interspersed with Great Plains badlands and wooded draws and ravines (LANDFIRE 2013) and was primarily managed for cattle production. Vegetation was a mixture of mid and short grasses, with western wheatgrass (*Pascopyrum smithii*), little bluestem (*Schizachyrium scoparium*), needle-and-thread (*Hesperostipa comata*), Kentucky bluegrass (*Poa pratensis*), blue grama (*Bouteloua gracilis*), and crested wheatgrass (*Agropyron cristatum*) being the dominant graminoids. The three study years differed drastically in the amount of precipitation received. We obtained daily precipitation data from the National Oceanic and Atmospheric Association (NOAA) station in Sidney, MT, and calculated the amount of precipitation received annually (1 January–31 December) and during the sharp-tailed grouse breeding season (15 March–15 August). Annual precipitation was 419.3 mm in 2016, 216.4 mm in 2017, and 341.5 mm in 2018. Total precipitation during the breeding season was 268.7 mm in 2016, 105.2 mm in 2017, and 312.1 mm in 2018.

The study area was centered on an ~3,300-ha Upland Gamebird Enhancement Program (UGBEP) project established by the Montana Department of Fish, Wildlife and Parks in 1993 that included four separate 3-pasture Hormay rest-rotation systems (Hormay and Evanko 1958). In a given year, cattle were stocked in one pasture from May–July (growing season), then moved to a second pasture during August–October (post-growing season), while the third pasture was rested and the order of rotation was

shifted within each 3-pasture rest-rotation system the next year. Therefore, no pasture was grazed during the same season in consecutive years and pastures rested in the previous year theoretically should have had the most residual cover. Average pasture size in the four rest-rotation systems was 292 ± 116 ha. Pastures of surrounding ranches, which included both private land and 4 pastures located on U.S. Forest Service National Grasslands were managed with more commonly used livestock grazing systems, including both season-long systems (19 pastures, ~4,800 ha) and 2- and 3-pasture summer rotation systems (25 pastures, ~5,200 ha). Grazing occurred in season-long pastures from approximately May to early November, while cattle were stocked in the same pastures in summer rotation systems each year for the same 6–8-week period (approximately April–June, June–July or Aug–Nov). Average pasture sizes in the season-long and summer rotation systems were 242 ± 312 ha and 238 ± 335 ha, respectively. Stocking rates were controlled by landowners and lessees and averaged rates were 0.93 AUM ha⁻¹, 1.46 AUM ha⁻¹, and 0.76 AUM ha⁻¹ for rest-rotation, season-long, and summer rotation pastures, respectively. The range of stocking rates for grazed pastures was 0.38 – 3.25 AUM ha⁻¹, 0.17 – 4.28 AUM ha⁻¹, and 0.21 – 4.45 AUM ha⁻¹ for rest-rotation, season-long, and summer rotation pastures, respectively, and included similar distributions within each grazing system (Milligan et al., In press). Average stocking rates did not exceed the range of rates (1.11 – 1.48 AUM ha⁻¹) recommended by the Natural Resources Conservation Service (NRCS) for the most common ecological site (R058AE001MT) in the study area. Environmental variables, including topography, average vegetation productivity, soil type, vegetation canopy greenness as measured by

the Normalized Difference Vegetation Index (NDVI) in June 2018, and the variation in small-scale vegetation cover and structure were similar among grazing systems (Milligan et al., In press, Milligan et al., In review).

METHODS

We captured grouse using walk-in funnel traps at 12 leks (5 in rest-rotation pastures, 3 in summer rotation pastures, and 4 in season-long pastures) during March–May in 2016–2018. Females were fitted with very high frequency (VHF) radio-transmitters (model A4050; Advanced Telemetry Systems, Isanti, MN). 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. All animal handling was approved under Montana State University’s Institutional Animal Care and Use Committee (Protocol #2016-01).

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 (Worton 1989) with the default smoothing parameter to calculate 95% home ranges 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. Habitat classifications utilized the 30-m resolution LANDFIRE data depicting vegetation 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 either the current or previous year. Stocking rate is a measure of the number of animals in a pasture during the entire grazing season. Within each home range, we calculated the mean stocking rate from both the current and previous year. As most females used more than one grazing

system, we calculated the proportion of each individual home range containing the three different grazing systems and assigned a female to the grazing system containing $\geq 60\%$ of the home range. Females were considered to use multiple systems if no one system accounted for $\geq 60\%$ of their home range and were not included in analyses evaluating the effect of grazing system.

We examined second-order habitat selection, or the selection of habitat for an individual's home range within the larger study area, using the adehabitat package in Program R to conduct compositional analysis of used versus available habitat (Johnson 1980, Aebischer et al. 1993). Available habitat was defined as the 95% home range calculated for all locations in a given year and each female's 95% home range represented the used space at an individual level. 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 an individual's home range, 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 vegetation type (LANDFIRE 2013). We used FRAGSTATS 4.2 (McGarigal 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 was chosen as it represents the average distance moved daily by female sharp-tailed grouse during the breeding season in our study.

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 (see Appendix E; 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 effect to account for potential autocorrelation among sampling points (Gillies et al. 2006, Thomas et al. 2006). For the four habitat covariates, we first selected the grain size at which selection was the strongest for each, basing

model selection comparing the 8 buffer distances on calculated leave-one-out information criterion (LOOIC) to identify a top model *sensu* Laforge et al. (2015). If error estimates overlapped for calculated LOOIC, we based model selection on calculated deviance information criteria (DIC) and considered > 5 DIC units to be a substantial difference in model fit (Thomas et al. 2006).

After assessing collinearity for each pair of explanatory variables ($r \geq 0.6$) and selecting the variable with the most support based on calculated LOOIC and DIC, we then evaluated support for all management and landscape variables in a full model using indicator variables. Regression coefficients for each variable were the product of binary indicator variables and both continuous and categorical covariates and we used the posterior distributions of the indicator variables to identify the variables with high inclusion probability that were the most important predictors of habitat selection (Kuo and Mallick 1997, O'Hara and Sillanpää 2009, Hooten and Hobbs 2015). 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 covariates represented the relationship between habitat variables and the relative probability of selection within the defined home range (Marzluff et al. 2004). 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 2016) in Program R 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 (Kéry 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 (O'Hara and Sillanpää 2009). 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 (Brooks and Gelman 1998, Gelman and Hill 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).

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 (Appendix F). Mean breeding season home range size for all females was 489 ± 41 ha but varied from 58–3,717 ha (Table 9). Variation in home range size was greatest in the rest-rotation system and smallest in the summer rotation system (Figure 11), but grazing system did not have a significant effect on home range size (Table 10). Density of edge habitat within the home range was the best predictor of home range size (Table 10) and was negatively related to the size of breeding season home ranges ($\beta = -5.26 \pm 1.48$; Figure 12).

At the second order, breeding season habitat use was ranked as follows: grassland = wooded draws >> other (primarily ruderal grasslands) >> cropland (Table 11), suggesting that females did not differentiate between grasslands and wooded draws with regards to preference but selected both habitat types over other habitats, including cropland. Females strongly selected for mixed grass prairie habitats, even though roughly 83% of the entire study area was composed of mixed grass prairie. Females strongly selected against cropland, 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 (see Appendix G). However, the proportion of grassland was correlated with both the proportion of cropland and the density of edge habitat (Appendix G), 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 (Figure 13). 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 (Figure 14). Furthermore, variability in selection as measured by σ^2 for each predictor variable was high, indicating large differences in individual habitat selection (Figure 15). A posterior predictive check suggested that the full model fit the data well, based on an estimated Bayesian p-value of 0.503.

DISCUSSION

Variation in home range size was very large among individuals and female sharp-tailed grouse selected home ranges in grasslands over other habitat types. Females strongly selected for mixed-grass prairie habitats, even though the majority of the study area was composed of mixed grass prairie, and average home range size declined with edge density. However, there was only marginal evidence that habitat selection within the home range increased with proximity to roads. There was no evidence for selection based on grazing management either when choosing home ranges or locations within home ranges. Importantly, high variability in both home range size and third-order selection

among individuals suggest highly plastic habitat use within the population and that individual-level selection was more important than population-level selection.

Home range sizes in our study were on average larger and more variable than those previously reported for sharp-tailed grouse, although previous studies were limited by sample size and often included male grouse (Christenson 1970, Saab and Marks 1992, Boisvert et al. 2005). Previous estimates of home ranges for sharp-tailed grouse have come primarily from shrub-steppe or forested regions and our home range estimates are more in line with those from prairie-chickens in the Great Plains that had larger home ranges with more variation among individuals (Patten et al. 2011, Winder et al. 2015, Winder et al. 2017). Home range size was negatively related to the density of edge habitat, suggesting that females could use a smaller area to meet their basic needs in more diverse habitats. Females also selected for patches of grassland at broad spatial scales, which is consistent with previous studies that found grouse selecting for grassland (Ryan et al. 1998, Niemuth 2003, Winder et al. 2015), although the negative relationship between home range size and edge density suggests that grouse also select habitats other than grassland.

In contrast to selection of home ranges, we found only weak selection for habitat features within the home range, contrasting with previous studies that have found small-scale selection based on vegetation features (Saab and Marks 1992, Goddard et al. 2009, Matthews et al. 2011). However, our habitat variables consisted only of remotely-sensed data and may have missed small-scale variation in vegetation structure or composition. Previous studies have also found consistent negative effects of anthropogenic

development on grouse habitat selection (Hagen et al. 2011, Dinkins et al. 2014b, Winder et al. 2014b), which contrasts with our results that found no effect of oil development and only a weak effect of distance to road on habitat selection. However, the distribution of anthropogenic disturbance was not even across our study area, with some individuals encountering few to no roads or oil wells, which could explain why there was no population-level selection. Furthermore, grouse habitat selection based on both landcover and anthropogenic disturbance such as roads has been shown to vary among studies and even sites within a single study (Cope 1992, Ryan et al. 1998, Goddard et al. 2009, Winder et al. 2014b, Winder et al. 2015, Winder et al. 2017), which can complicate population-level inferences.

There was no evidence for selection of a home range based on grazing system or for third-order selection relative to grazing management, despite significant variation in precipitation among years. When selecting a home range, females did not differentiate among grazing systems and there was no evidence that selection differed from random. Females also showed no selection for either grazing system or stocking rate when selecting habitat within the home range. Females did not differ in selection between the specialized rest-rotation system and other commonly employed systems, which contrasts with previous work on a similar heterogeneity-based management strategy that found that greater prairie-chickens selected for areas within the patch-burn grazing system (Winder et al. 2017). There was no evidence for an effect of stocking rate, which conflicts with previous studies that have documented consistently negative effects of high stocking rates on prairie-chickens (McNew et al. 2015, Kraft 2016, Winder et al. 2018). However,

stocking rates were below or within the range recommended by the NRCS for our study area and it is possible that selection may only be apparent across a broader range of stocking rates. Furthermore, no grazing system increased variation in vegetation cover at the moderate stocking rates in our study area relative to other systems evaluated (Milligan et al., In press, Milligan et al., In review), and previous studies have found that small-scale habitat selection by grouse was primarily driven by available cover (Saab and Marks 1992, Goddard et al. 2009, Matthews et al. 2011). Our study area is also naturally heterogeneous both edaphically and topographically, which may have created sufficient variation in cover across the landscape regardless of management.

While there was only weak evidence for population-level selection at the third order, there was significant individual variation in habitat selection, suggesting that individual-level differences were driving habitat selection rather than population-level patterns. Significant individual variation is consistent with previous work suggesting that habitat selection can vary by year or weather conditions and can vary across spatial scales (Winder et al. 2015, Winder et al. 2017). Taken together, this suggests that generalized habitat recommendations across sites and related species may not be appropriate. Furthermore, random-intercept models may be appropriate if population-level inferences are of interest, but random-coefficient models should be explored to capture the full degree of individual variation (Gillies et al. 2006, Leclerc et al. 2016). The variation in habitat selection behavior could suggest a strategy of “unlimited plasticity”, such that any individual is capable of changing their habitat selection in response to surrounding environmental conditions (Sih et al. 2004). In contrast, if individual differences are

consistent across time, then those differences can represent alternative approaches that evolved to respond to a variable environment (McLoughlin et al. 2006, Leclerc et al. 2014). Regardless, if individual differences are correlated with fitness, both strategies can have ecological and evolutionary implications (Réale et al. 2010, Sih et al. 2012). Future research should explore both the consistency in individual differences across time and the link between individual differences and fitness.

CONCLUSIONS

At a broad scale, female sharp-tailed grouse selected home ranges in grassland but showed little to no selection for habitat or management variables when selecting locations within their home ranges. Furthermore, females exhibited no selection for the rest-rotation grazing system, which, in theory, could create pasture-level heterogeneity and thus improve habitat quality, compared to other grazing systems. This suggests that, at moderate stocking rates, rest-rotation grazing may not be increasing pasture-level heterogeneity relative to other grazing systems as hypothesized and so alternative grazing strategies may not have a significant influence on sharp-tailed grouse habitat selection in the northern mixed-grass prairie. Furthermore, female sharp-tailed grouse exhibited strong individual differences in both home range size and third-order habitat selection that outweighed any potential population-level trends, suggesting that specific management recommendations are inappropriate, particularly across large spatial scales. Combined with the strong selection for large patches of mixed grass prairie, our results suggest that maintaining economically viable ranching strategies with moderate stocking

rates that keep diverse native grasslands on the landscape may be the best conservation approach for sharp-tailed grouse.

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

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

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

Model	K	AIC _c	Δ AIC _c	AIC _c w_i	Cum. w_i	LogLik
Edge density	3	2157.27	0.00	0.93	0.93	-1075.55
Dist. to grassland edge	3	2165.05	7.78	0.02	0.95	-1079.44
Nest outcome	3	2165.25	7.98	0.02	0.96	-1079.54
Null	2	2166.80	9.53	0.01	0.97	-1081.36
Year	3	2167.47	10.20	0.01	0.98	-1080.65
% Rest-rotation	3	2167.71	10.43	0.01	0.98	-1080.77
Stocking rate	3	2168.12	10.84	0.00	0.99	-1080.97
% Summer rotation	3	2168.14	10.87	0.00	0.99	-1080.98
Dist. to lek	3	2168.65	11.38	0.00	0.99	-1081.24
Dist. to road	3	2168.73	11.46	0.00	0.99	-1081.28
Dist. to oil pad	3	2168.84	11.57	0.00	1.00	-1081.33
Prop. grassland	3	2168.88	11.61	0.00	1.00	-1081.36

Table 11. Simplified ranking matrix of female sharp-tailed grouse breeding season habitat selection based on landcover 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

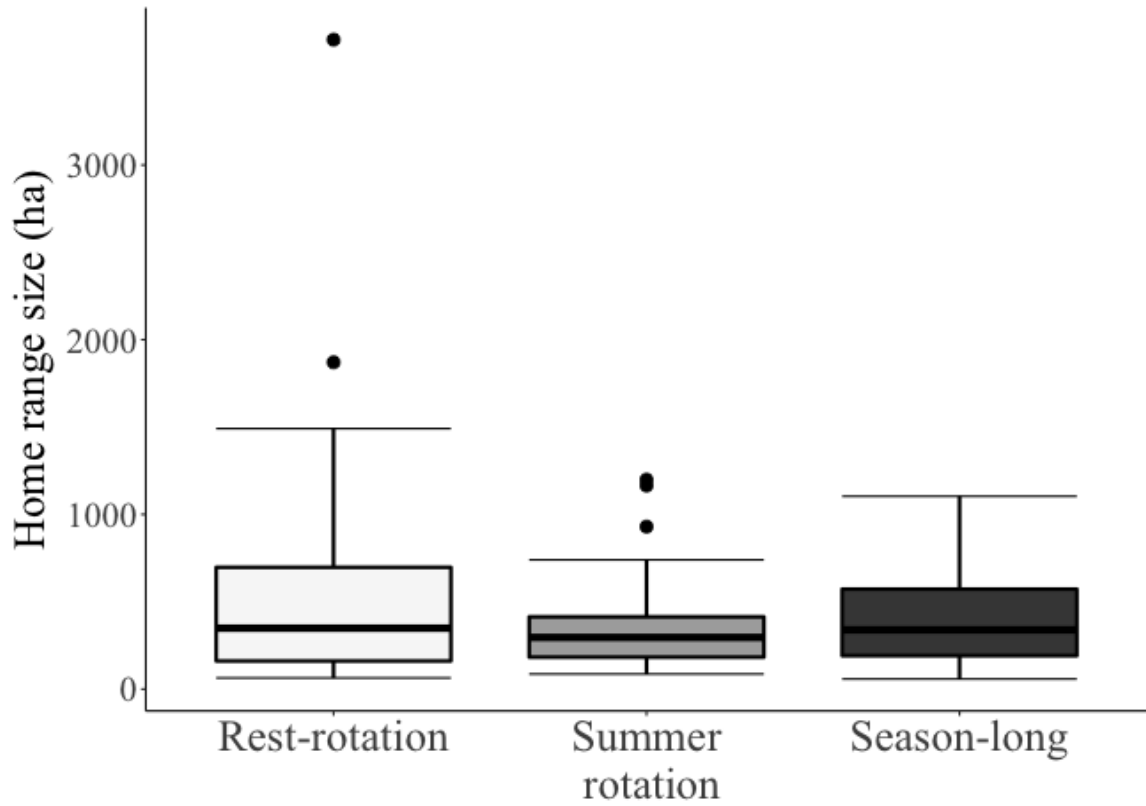


Figure 11. Female sharp-tailed grouse breeding season home range size (\pm SE) by grazing system. An individual female was assigned to a grazing system according to the system containing $\geq 60\%$ of the individual's home range.

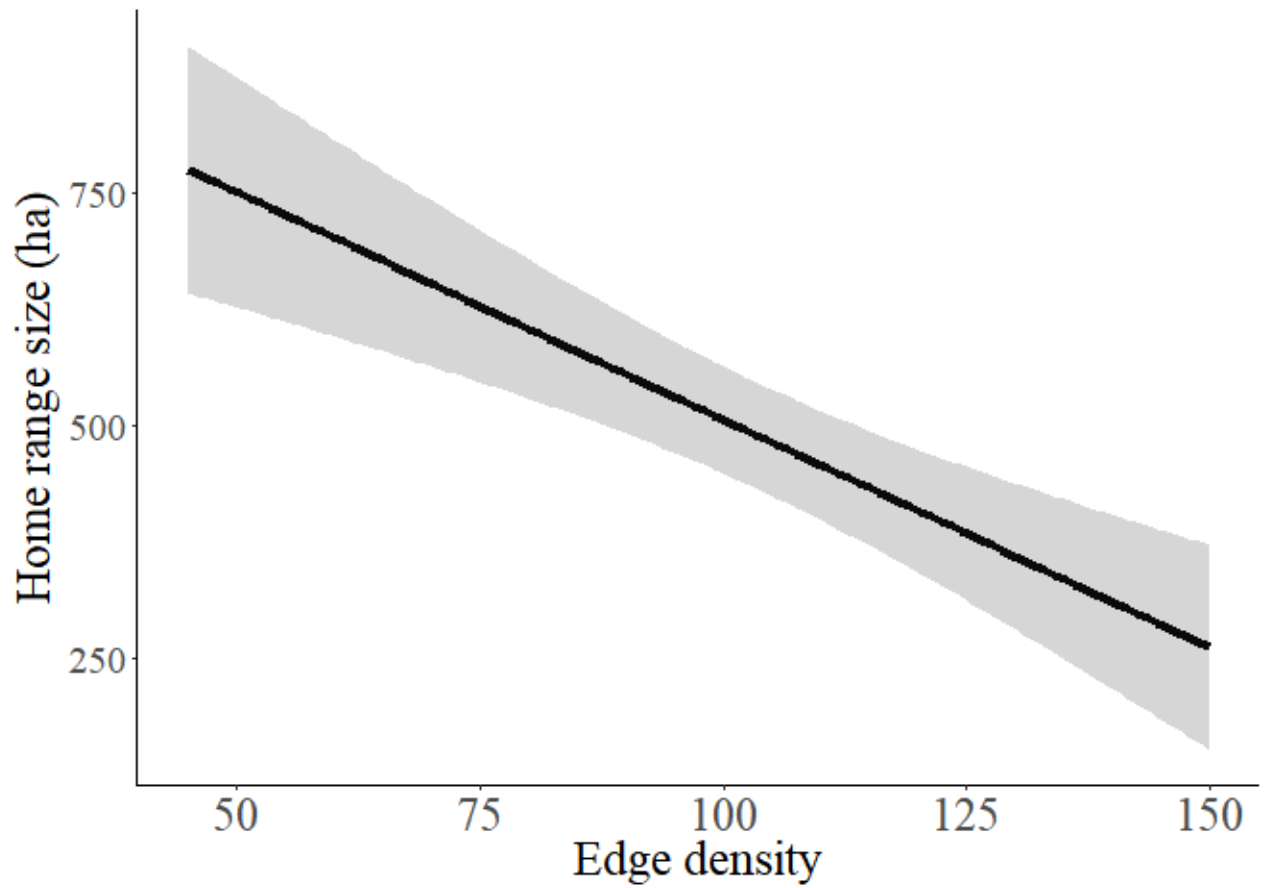


Figure 12. Relationship (\pm 85% confidence intervals) between the density of edge habitat (total landcover edge length / polygon area) and breeding season home range size for female sharp-tailed grouse.

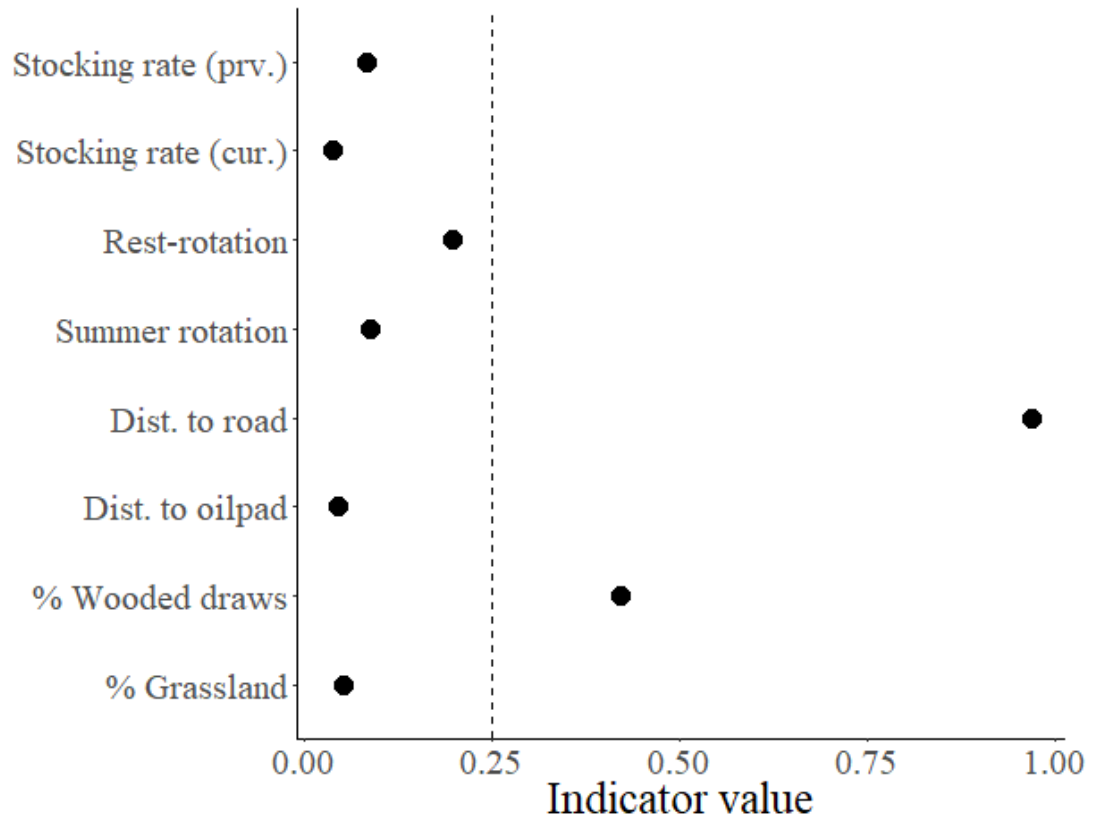


Figure 13. Bayesian variable selection identifying important predictors of sharp-tailed grouse third-order habitat selection during the breeding season. Predictors with indicator variables ≤ 0.25 are considered unimportant.

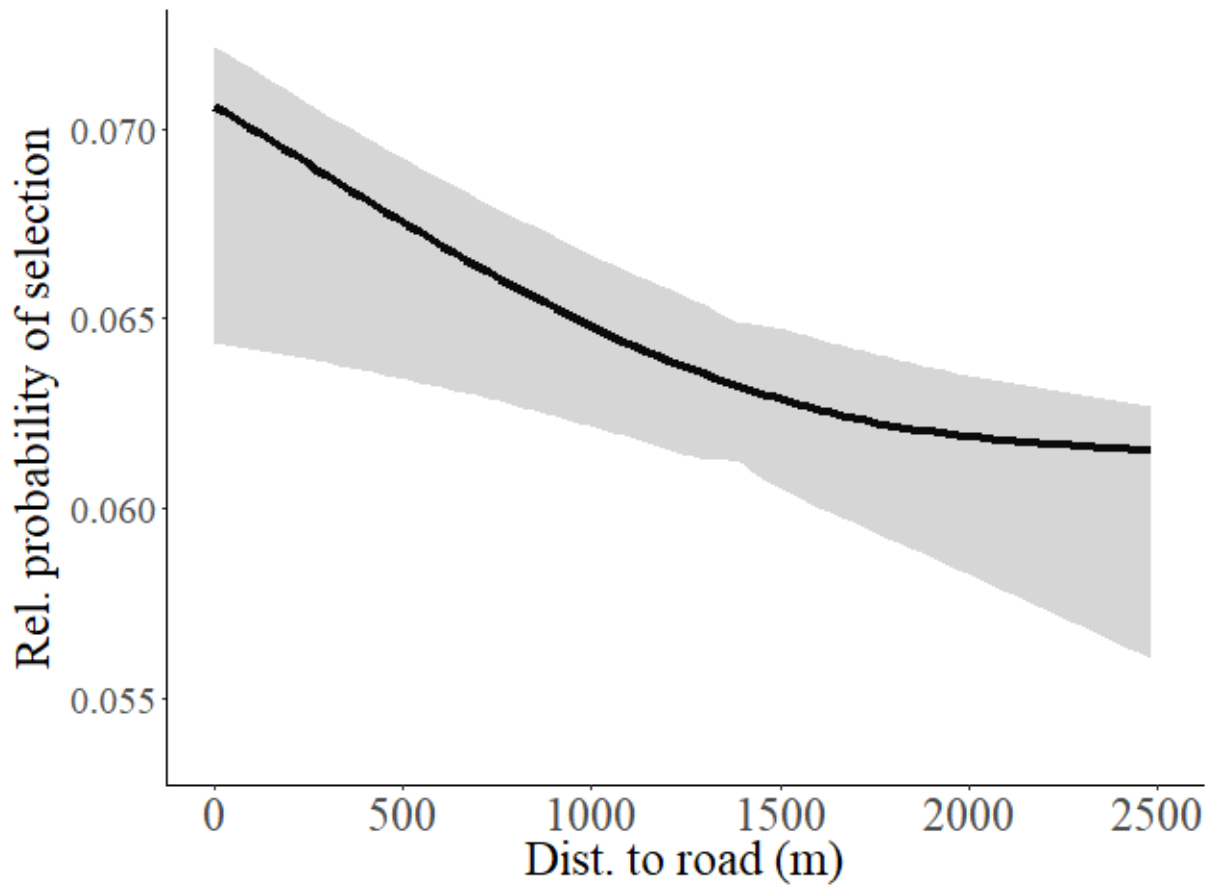


Figure 14. Relationship (\pm 95% credible intervals) between the distance to a road and the relative probability of selection of female sharp-tailed grouse within the breeding season home range.

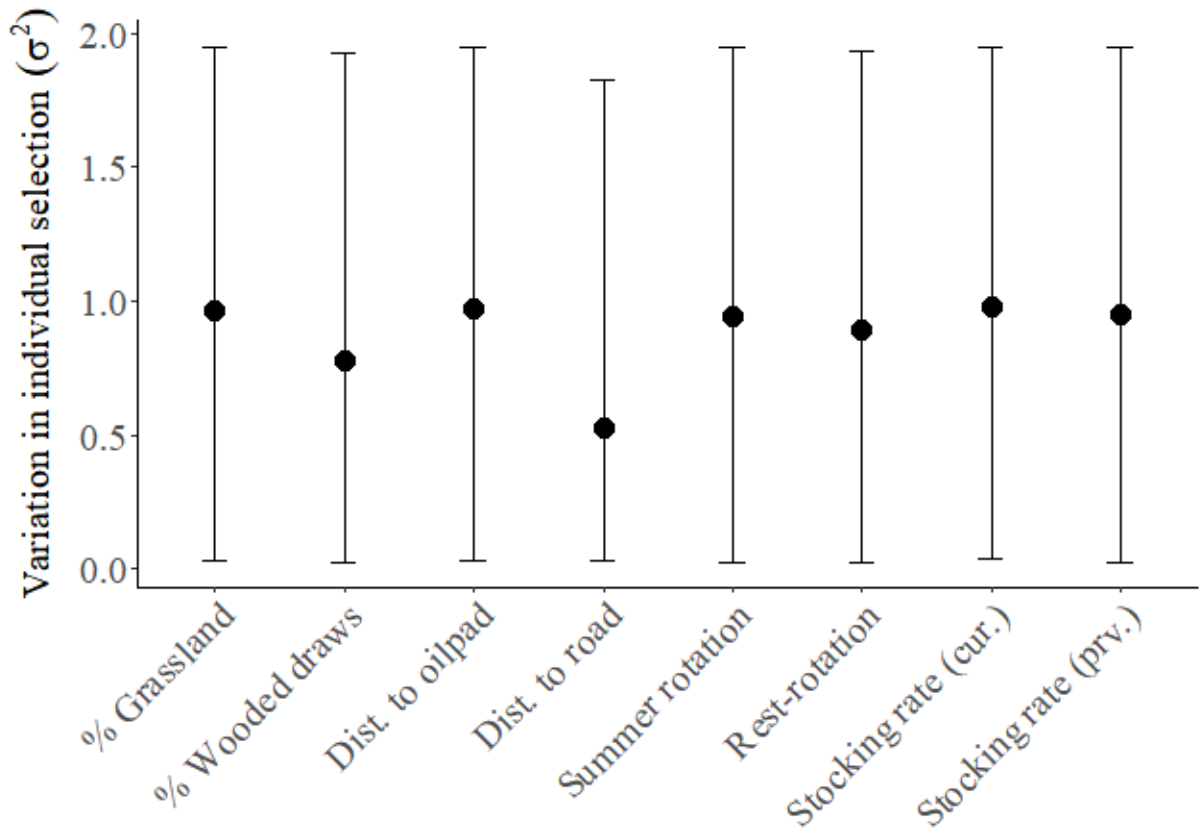


Figure 15. Posterior estimates of the variability in selection ($\sigma^2 \pm 95\%$ credible intervals) among individual female sharp-tailed grouse for each habitat variable. σ^2 is a measure of how strongly individuals varied in selection for different habitat variables. Habitat variables were scaled prior to model fitting.

CHAPTER FIVE

CONCLUSION AND MANAGEMENT RECOMMENDATIONS

Livestock grazing is a dominant land use worldwide, occurring on 70% of the land in western North America (Fleischner 1994, Krausman et al. 2009, Alkemade et al. 2013), and can directly and indirectly influence ecosystem composition, function, structure, and productivity (Fleischner 1994, Boyd et al. 2014). While overgrazing has been linked to the decline of many wildlife populations, (Fleischner 1994), many grassland species co-evolved with large grazing animals, with species requiring habitats along the entire structural gradient created by different intensities of grazing (Samson and Knopf 1996, Derner et al. 2009). As a result, bird species diversity is often higher in grasslands managed for structural and compositional heterogeneity in vegetation than in areas managed with intensive early stocking systems that promote uniform utilization (Coppedge et al. 2008), although stocking rates and precipitation may mediate the impacts of specific grazing systems (Briske et al. 2008, Lipsey and Naugle 2017, Vold 2018). Thus, certain grazing regimes that increase structural and compositional heterogeneity could potentially provide a mosaic of patches in different stages of recovery from disturbance by livestock (Ryder 1980, Fuhlendorf and Engle 2001, Coppedge et al. 2008, Krausman et al. 2009). Rest-rotation grazing was originally developed to improve range condition (Hormay and Evanko 1958), but it could conceptually function as a conservation strategy to mimic historic disturbance regimes and create pasture-level heterogeneity in the absence of fire (Frisina 1991, Montana Department of Fish, Wildlife & Parks 2011). Studies examining the direct effects of

grazing on prairie grouse populations, however, are limited (Grosz and Kirby 1986, Krausman et al. 2009, Dettenmaier et al. 2017).

Sharp-tailed grouse (*Tympanuchus phasianellus*) are recognized as an indicator species for grassland habitats because their habitat requirements encompass a wide range of vegetation structure and composition, with short, bare areas used for lekking; denser, herbaceous cover for nesting; and thicker shrubs for winter cover and food (Marks and Marks 1988, Derner et al. 2009). Therefore, identifying appropriate grazing management strategies to conserve sharp-tailed grouse populations could have implications for a suite of grassland species (Hillman and Jackson 1973, Poiani et al. 2001, Roersma 2001). Our research used sharp-tailed grouse as a model species to evaluate rest-rotation grazing as a conservation management technique compared to other commonly employed grazing systems, including summer rotation and season-long grazing. Our specific objectives were to assess the effects of different grazing systems and stocking rates on 1) the nest site selection and nest survival of sharp-tailed grouse, 2) the survival and habitat-associated mortality risk of adult female sharp-tailed grouse, and 3) second- and third-order breeding season habitat selection of female sharp-tailed grouse.

Grazing system did not significantly influence either nest site selection or nest survival of sharp-tailed grouse and overall nest survival was similar even among the three treatments within the rest-rotation system (grazed during the growing season, grazed post-growing season, rested entire year). Both nest site selection and nest survival were strongly associated with visual obstruction at the nest site, which is a measure of nest concealment and biomass (Robel et al. 1970). While stocking rate had a biologically

meaningful influence on visual obstruction, effects of grazing system were minimal, which concurs with previous reviews of the effects of rangeland management approaches on vegetation (Briske et al. 2008, Briske et al. 2011). Previous research that found an effect of grazing management on nesting grouse either found a strong link between grazing variables and local habitat, or only evaluated grazing management without controlling for habitat variables (McNew et al. 2015, Kraft 2016), while our results are more in line with a study in central Montana that found negligible effects of grazing management on both vegetation and greater sage-grouse (*Centrocercus urophasianus*) nest survival (Smith et al. 2018a;b).

In addition, variation in vegetation cover within each grazing system was larger than differences among systems, suggesting that the rest-rotation grazing was not creating pasture-level heterogeneity. The selective foraging of cattle at moderate stocking rates like those found in our study area can create significant vegetation heterogeneity within a pasture regardless of grazing system, particularly in rangelands with inherent topographical and edaphic variation (Bailey et al. 1998, Fuhlendorf and Engle 2001). We found strong evidence that grouse were selecting nest sites at a very small spatial scale based on the vegetation cover at the nest bowl itself. This coincides better with patch-scale heterogeneity created by the selective foraging of cattle rather than any potential larger-scale pasture-level heterogeneity that could be created by rest-rotation grazing.

While we found no effect of grazing system on either nest site selection or nest survival, nest survival increased with pasture-level stocking density (AU ha^{-1}) while the nest was active, possibly due to the mitigating presence of cows or ranchers on nest

predators (Kluever et al. 2008, Foster et al. 2015). Previous studies have focused on the effects of grazing activity on nesting grouse by evaluating the indirect impacts on vegetation by measuring stocking rates or densities for the entire grazing period rather than during the period while the nest was active (McNew et al. 2015, Kraft 2016). However, stocking densities during the nesting period were relatively low in our study area (≤ 1.3 AU ha⁻¹ while nests were active) and at higher stocking densities the positive benefits of cow presence may be offset by indirect negative effects on vegetation cover.

While breeding season survival was consistent across years despite significant variation in precipitation during the study, we found no evidence for an effect of grazing management, including either grazing system or stocking rate, on breeding season survival or habitat-associated mortality risk. There were differences in the seasonal patterns of mortality risk among the three grazing systems that may represent trade-offs in the timing of mortality risk but corresponded to no effect on cumulative breeding season survival. This contrasts with previous research that found significant benefits for the annual survival of greater prairie-chickens (*Tympanuchus cupido*) in tallgrass prairie from the heterogeneity-focused management system of patch-burn grazing (Winder et al. 2018), but it is possible that rest-rotation grazing was not influencing variation in cover at a spatial scale relevant to grouse in the less productive mixed-grass prairie. In contrast to previous studies finding consistently negative effects of high stocking rates, we found no evidence for an effect of stocking rate on adult female survival (Kraft 2016, Dettenmaier 2018, Winder et al. 2018). Stocking rates did not exceed recommended rates for our study area, though, and an impact on mortality risk may only be seen at higher stocking

rates. A more important correlate of sharp-tailed grouse survival was the amount of cropland in the landscape, which is consistent with previous studies (Ryan et al. 1998, Manzer 2004, Smith et al. 2016). The majority of mortalities in our study was due to predation, and landscapes with greater proportions of cropland are more fragmented and can sustain larger populations of common grouse predators like coyotes (Andr n 1995, Kurki et al. 1998, Winter et al. 2000).

Grazing management was also not a strong driver of habitat selection at either spatial scale examined, including the selection of an individual's home range within the larger study area and the selection of habitat within the home range. When choosing a home range, female sharp-tailed grouse strongly selected for mixed-grass prairie habitats, even though the majority of the study area was composed of mixed-grass prairie. Females did not differentiate between the three grazing systems, with the selection of home ranges relative to grazing system being no different than random. This contrasts with a previous study that found that greater prairie-chickens selected for areas within the heterogeneity-based patch-burn grazing system compared to intensive early stocking, which incorporates similar stocking rates to season-long systems but concentrates grazing activity during the first half of the growing season (Winder et al. 2017). In addition, we found no evidence for an effect of stocking rate (AUM ha^{-1}), which contradicts the results of previous studies that found consistently negative effects of high stocking rates on prairie grouse (McNew et al. 2015, Kraft 2016, Winder et al. 2018). However, average stocking rates were within the range recommended by the Natural Resources Conservation Service (NRCS) as moderate in our study area and grazing system did not

significantly influence vegetation cover, which may explain the lack of selection based on grazing management.

In contrast to the strong selection for mixed-grass prairie when choosing home ranges, we found only weak selection for habitat features and no evidence for selection based on grazing management within the home range. This contradicts previous studies that found small-scale selection of vegetation features (Saab and Marks 1992, Goddard et al. 2009, Matthews et al. 2011) and anthropogenic development (Hagen et al. 2011, Dinkins et al. 2014b, Winder et al. 2014b). Importantly, however, there was significant variability in both home range size and third-order selection among individuals, which suggests highly plastic habitat use within a population rather than any population-level patterns. In addition, grouse habitat selection has been shown to vary both among studies and even sites within a single study, which can complicate or outweigh population-level inferences (Cope 1992, Ryan et al. 1998, Goddard et al. 2009, Winder et al. 2014b, Winder et al. 2015, Winder et al. 2017).

Taken together, our results suggest that rest-rotation grazing did not have a meaningful influence on any aspect of sharp-tailed grouse ecology we studied, including both habitat selection and multiple population parameters, relative to other grazing systems. Vegetation cover, which was the most important driver of nest survival, was more variable within each grazing system than among systems, suggesting that rest-rotation grazing was not increasing pasture-level heterogeneity relative to other grazing systems as hypothesized. In addition, heterogeneity at a small spatial scale was more important, specifically for nesting grouse, suggesting that drivers of small-scale

vegetation heterogeneity, including the selective foraging of cattle and inherent topographic and edaphic variability, were more relevant. In contrast, we did find evidence for a negative effect of stocking rate on vegetation cover, which is consistent with previous reviews (Briske et al. 2008, Briske et al. 2011), and previous research suggests that wildlife responses to grazing management can be mediated by factors including precipitation and productivity (Lipseý and Naugle 2017, Monroe et al. 2017, Vold 2018). Therefore, specific management recommendations beyond maintaining moderate stocking rates may not be appropriate, particularly across large spatial scales. However, average stocking rates did not exceed the range recommended by the NRCS as moderate for our study area, and effects of grazing management on grouse should be assessed across a larger range of stocking rates. Future research should also evaluate the effects of both rest-rotation and other grazing management approaches at additional sites and further evaluate factors mediating wildlife responses to management regimes.

Although we did not find any evidence for an effect of grazing management, our results suggest that sharp-tailed grouse in our study population exhibited highly plastic habitat selection. This variation in habitat selection behavior could imply high phenotypic plasticity where individual animals are capable of altering their behavior in response to the environmental conditions they experience (Sih et al. 2004, Nussey et al. 2007). In contrast, if differences in behavior are consistent within individuals across time, then those differences could represent alternative approaches within a population to deal with a variable environment (McLoughlin et al. 2006, Wolf and Weissing 2012, Leclerc et al. 2014). Regardless, if individual differences are linked to fitness outcomes, such variation

could have both ecological and evolutionary implications (Nussey et al. 2007, Sih et al. 2012, Wolf and Weissing 2012, Merrick and Koprowski 2017). Individual differences can affect demographic parameters, population dynamics, population responses to disturbance, and the success of conservation and management actions (Sih et al. 2012, Wolf and Weissing 2012, Merrick and Koprowski 2017). For example, individuals can differ in both the magnitude and pattern of their movements, which, in turn, can influence gene flow, population dynamics, and the distribution of species (Bowler and Benton 2005, Wolf and Weissing 2012, Merrick and Koprowski 2017). Nevertheless, despite their potential to alter both ecological and evolutionary dynamics, individual differences are rarely considered in habitat restoration or management efforts (Merrick and Koprowski 2017). In theory, high variation in individual behavior should allow a species to survive across a broader range of environmental conditions and cope with both spatial and temporal variation in conditions (Sih et al. 2012). Therefore, providing sufficient habitat heterogeneity to support diverse individual differences in behavior should be considered in management actions (Sih et al. 2012, Smith and Blumstein 2013, Merrick and Koprowski 2017). In addition, given increasing concern over the consequences of human-induced environmental change, research into how individual differences influence population-level responses will improve our understanding of the ability of natural systems to handle environmental change (Nussey et al. 2007). Future research should evaluate both between- and within-individual variation in behavior (Dingemanse and Dochtermann 2013).

Despite high variation in small-scale habitat selection among individuals, however, female grouse strongly selected for mixed-grass prairie at large spatial scales. In addition, mortality risk was primarily driven by the amount of cropland in the surrounding landscape. Cropland conversion can decrease and fragment remaining grassland habitats and represents the most significant threat to grassland wildlife (Hoekstra et al. 2005, Stephens et al. 2008). This, combined with the lack of a system-level effect of grazing management in our study, suggests that preserving large intact grasslands is a better conservation strategy for sharp-tailed grouse than prescribing specific grazing systems, particularly given recent research suggesting that the effect of stocking rate outweighs any system-level effects of grazing management and given that precipitation mediates grazing effects on avian responses (Briske et al. 2008, Briske et al. 2011, Lipsey and Naugle 2017, Vold 2018). Therefore, economically viable ranching strategies with moderate stocking rates that allow diverse native grasslands to remain on the landscape should be prioritized over specific grazing management strategies to improve habitat for sharp-tailed grouse.

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APPENDICES

APPENDIX A

SUPPORTING INFORMATION FOR STOCKING RATE ANALYSES

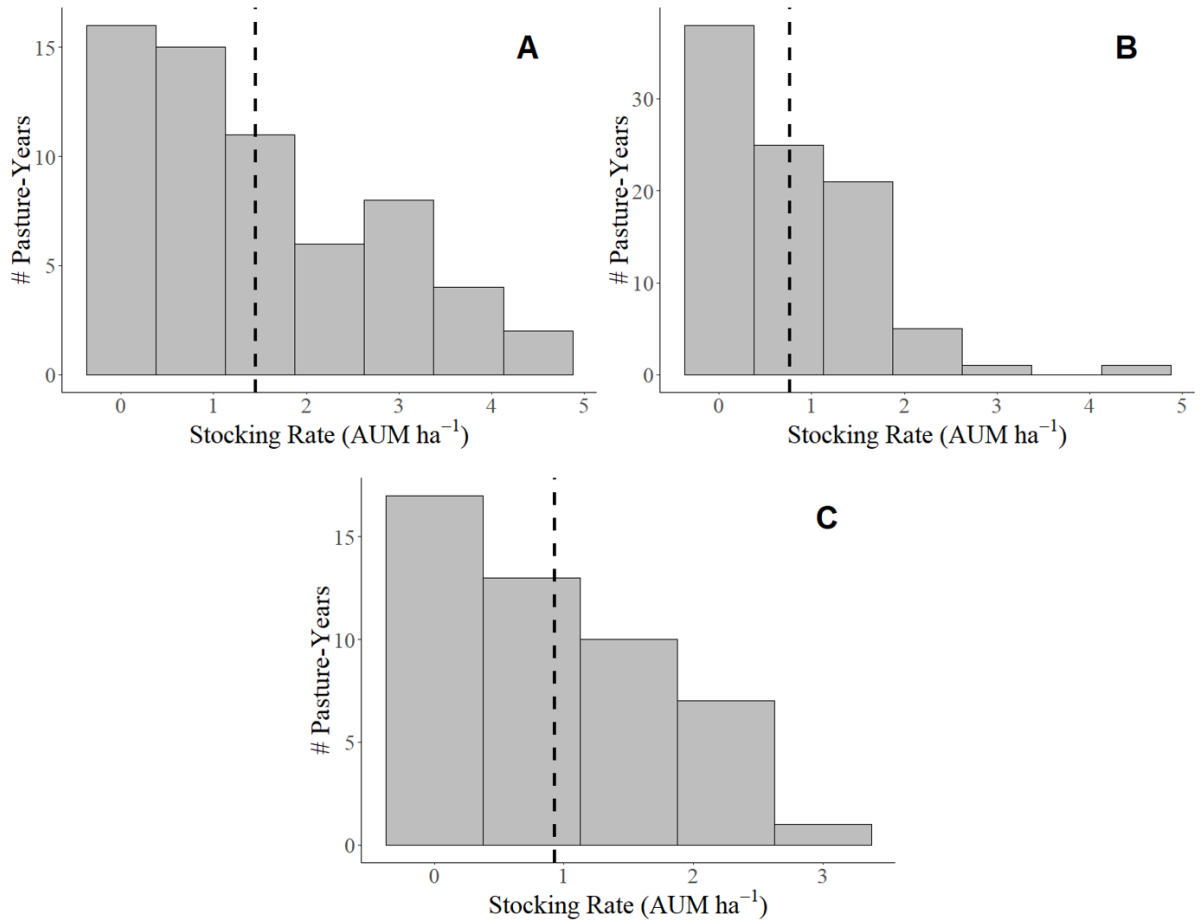


Figure A1. Distribution of stocking rates in each pasture in each year by grazing system: season-long (A), summer rotation (B), and rest-rotation (C). Vertical dashed lines denote the mean stocking rate in each grazing system.

APPENDIX B

SUPPORTING INFORMATION FOR NEST SITE SELECTION ANALYSIS

Table B1. Multicollinearity results for nest-scale habitat variables in the nest site selection analysis.

	ln(Nest VOR)	% Residual	% New Grass	% Forb	% Shrub
% Residual	0.09				
% New Grass	0.13	0.27			
% Forb	0.09	-0.03	-0.04		
% Shrub	0.16	-0.17	-0.18	-0.09	
Dist. to Grassland Edge	0.08	0.11	0.05	0.03	-0.05

Table B2. Multicollinearity results for home range-scale habitat variables in the nest site selection analysis.

	MSI	Dist. to Oil Pad	Edge Density	Dist. to Road	Prop. Grassland
Dist. to Oil Pad	0.41				
Edge Density	0.76	0.42			
Dist. to Road	-0.24	-0.33	-0.33		
Prop. Grassland	-0.74	-0.64	-0.83	0.52	
Dist. to Lek	0.03	0.15	0.26	-0.03	-0.09

Table B3. Multicollinearity results for habitat variables included in the multi-scale nest site selection analysis.

	MSI	ln(Nest VOR)	% New Grass	% Residual
ln(Nest VOR)	0.06			
% New Grass	0.05	0.13		
% Residual	0.11	0.09	0.27	
% Shrub	0.15	0.16	-0.18	-0.17

Table B4. Multicollinearity results for habitat and management variables included in the full nest site selection analysis.

	ln(Nest VOR)	% Residual	MSI
% Residual	0.09		
MSI	0.06	0.11	
Stocking Rate (prv. yr.)	-0.19	-0.14	0.03

Table B5. Support for candidate models evaluating functional relationships between visual obstruction and nest site selection of sharp-tailed grouse. The number of parameters (K), AIC_c values, ΔAIC_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
ln(Nest VOR)	3	303.94	0.00	0.94	0.94	-148.94
Nest VOR + Nest VOR ²	4	309.58	5.64	0.06	1.00	-150.74
Nest VOR	3	331.98	28.04	0.00	1.00	-162.96
ln(VOR)	3	437.14	133.20	0.00	1.00	-215.54
VOR + VOR ²	4	437.82	133.88	0.00	1.00	-214.86
VOR	3	466.57	162.63	0.00	1.00	-230.25
Null	2	528.04	224.10	0.00	1.00	-262.00

Table B6. Support for candidate models predicting sharp-tailed grouse nest site selection based on underlying variables in 2016–18. The number of parameters (K), AIC_c values, ΔAIC_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
Null	2	528.04	0.00	0.53	0.53	-262.00
Female Age	3	529.90	1.86	0.21	0.73	-261.92
Nest Attempt	3	530.04	2.00	0.19	0.93	-261.99
Year	4	531.96	3.92	0.07	1.00	-261.92

Table B7. Support for candidate models predicting sharp-tailed grouse nest site selection at the nest site level in 2016–18. The number of parameters (K), AIC_c values, ΔAIC_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
ln(Nest VOR) + %New Grass + %Residual + %Shrub	6	293.20	0.00	0.61	0.61	-140.49
ln(Nest VOR) + %Residual	4	294.22	1.02	0.37	0.98	-143.06
ln(Nest VOR) + %Forb	4	301.41	8.21	0.01	0.99	-146.65
ln(Nest VOR)	3	303.94	10.74	0.00	1.00	-148.94
ln(Nest VOR) + %Shrub	4	304.09	10.89	0.00	1.00	-147.99
ln(Nest VOR) + % New Grass	4	305.88	12.68	0.00	1.00	-148.89
%Bare	3	477.25	184.05	0.00	1.00	-235.59
%New Grass + %Residual + %Shrub	5	483.56	190.36	0.00	1.00	-236.70

%New Grass + %Forb + %Residual + %Shrub	6	485.62	192.42	0.00	1.00	-236.70
%Shrub	3	497.65	204.45	0.00	1.00	-245.79
%Residual	3	521.14	227.94	0.00	1.00	-257.54
Null	2	528.04	234.84	0.00	1.00	-262.00
Dist. to Grassland Edge	3	529.09	235.89	0.00	1.00	-261.51
%Forb	3	529.60	236.40	0.00	1.00	-261.77
%New Grass	3	529.73	236.53	0.00	1.00	-261.83

Table B8. Support for candidate models predicting sharp-tailed grouse nest site selection at the home range level in 2016–18. The number of parameters (K), AIC_c values, Δ AIC_c values, model weights (w_i) and log-likelihoods are reported.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. w_i	LogLik
Mean Shape Complexity	3	524.93	0.00	0.56	0.56	-259.43
Null	2	528.04	3.11	0.12	0.67	-262.00
Dist. to Oil Pad	3	528.24	3.32	0.11	0.78	-261.09
Edge Density	3	528.64	3.72	0.09	0.87	-261.29
Dist. to Road	3	529.86	4.93	0.05	0.91	-261.90
Prop. Grassland	3	530.03	5.11	0.04	0.96	-261.99
Dist. to Lek	3	530.04	5.11	0.04	1.00	-261.99

APPENDIX C

SUPPORTING INFORMATION FOR NEST SURVIVAL ANALYSIS

Table C1. Multicollinearity results for the underlying variables in the nest survival analysis.

	Growing Season Precip.	Available Precip.
Available Precip.	-0.99	
Female Condition	0.13	-0.07

Table C2. Multicollinearity results for nest-scale habitat variables in the nest survival analysis.

	ln(VOR)	% Residual	% New Grass	% Forb	% Shrub	% Bare
% Residual	-0.28					
% New Grass	-0.15	0.26				
% Forb	0.06	0.03	0.00			
% Shrub	0.38	-0.34	-0.23	-0.08		
% Bare	0.09	-0.16	-0.09	0.07	-0.12	
Dist. to Grassland Edge	-0.09	0.09	0.04	0.17	-0.08	-0.19

Table C3. Multicollinearity results for home range-scale variables in the nest survival analysis.

	Dist. to Road	Prop. Grassland	MSI	Edge Density
Prop. Grassland	0.49			
MSI	-0.31	-0.78		
Edge Density	-0.26	-0.84	0.83	
Dist. to Oil Pad	-0.29	-0.63	0.44	0.38

Table C4. Multicollinearity results for the habitat variables included in the multi-scale nest survival analysis.

	ln(VOR)	% Residual	% New Grass	% Forb	Prop. Grassland
% Residual	-0.28				
% New Grass	-0.15	0.26			
% Forb	0.06	0.03	0.00		
Prop. Grassland	-0.28	0.22	-0.09	0.09	
Dist. to Road	0.03	0.17	-0.04	0.06	0.49

Table C5. Multicollinearity results for management variables included in the nest survival analysis.

	Stocking Rate (cur. yr.)	Stocking Rate (prv. yr.)
Stocking Rate (prv. yr.)	0.05	
Stocking Density	0.03	0.18

Table C6. Multicollinearity results for the habitat and management variables included in the full nest survival analysis.

	ln(VOR)	Prop. Grassland
Prop. Grassland	-0.28	
Stocking Density	0.22	-0.29

Table C7. Support for candidate models evaluating functional relationships between visual obstruction and sharp-tailed grouse nest survival in 2016–18. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and deviance are reported.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Deviance
ln(VOR)	2	753.59	0.00	0.54	749.59
VOR	2	755.57	1.98	0.20	751.57
VOR + VOR ²	3	756.61	3.02	0.12	750.60
ln(Nest VOR)	2	758.40	4.81	0.05	754.40
Null	1	758.94	5.35	0.04	756.94
Nest VOR	2	759.59	6.00	0.03	755.59
Nest VOR + Nest VOR ²	3	759.87	6.28	0.02	753.87

Table C8. Support for candidate models predicting sharp-tailed grouse nest survival in 2016–18 based on underlying variables. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and deviance are reported.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Deviance
Growing Season Precip.	2	758.20	0.00	0.25	754.19
Null	1	758.94	0.75	0.17	756.94
Available Precip.	2	759.05	0.85	0.16	755.05
Female Condition	2	760.19	1.99	0.09	756.19
Daily Precip.	2	760.36	2.16	0.09	756.35
Nest Attempt	2	760.56	2.36	0.08	756.56

Female Age	2	760.62	2.43	0.08	756.62
Female Condition + Age	3	761.74	3.55	0.04	755.74
Female Age + Nest Attempt	3	762.20	4.00	0.03	756.19

Table C9. Support for candidate models predicting sharp-tailed grouse nest survival in 2016–18 at the nest site scale. The number of parameters (K), AIC_c values, Δ AIC_c values, model weights (w_i) and deviance are reported.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Deviance
ln(VOR)	2	753.59	0.00	0.33	749.59
ln(VOR) + %Forb	3	754.09	0.50	0.26	748.08
ln(VOR) + %Residual	3	755.41	1.82	0.13	749.41
ln(VOR) + %New Grass	3	755.42	1.83	0.13	749.42
ln(VOR) + %Forb + %New Grass + %Residual	5	757.52	3.93	0.05	747.50
Null	1	758.94	5.35	0.02	756.94
%Forb	2	759.25	5.66	0.02	755.25
%Bare	2	759.58	5.99	0.02	755.58
Dist. to Grassland Edge	2	760.10	6.51	0.01	756.10
%New Grass	2	760.70	7.11	0.01	756.70
%Residual	2	760.94	7.35	0.01	756.94
%Forb + %New Grass + %Residual	4	763.91	10.32	0.00	755.90
%Forb + %New Grass + %Residual + %Shrub	5	764.38	10.79	0.00	754.36

Table C10. Support for candidate models predicting sharp-tailed grouse nest survival in 2016–18 at the home range scale. The number of parameters (K), AIC_c values, Δ AIC_c values, model weights (w_i) and deviance are reported.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Deviance
Dist. to Road	2	757.17	0.00	0.35	753.17
Prop. Grassland	2	758.53	1.36	0.18	754.53
Null	1	758.94	1.77	0.14	756.94
Mean Shape Complexity	2	758.99	1.81	0.14	754.98
Edge Density	2	759.23	2.05	0.13	755.22
Dist. to Oil Pad	2	760.60	3.43	0.06	756.60

APPENDIX D

SUPPORTING INFORMATION FOR ADULT SURVIVAL ANALYSES

Table D1. Multicollinearity results for variables evaluated using Andersen-Gill models to assess mortality risk of female sharp-tailed grouse in eastern Montana and western North Dakota during the breeding season in 2016–2018.

	Stocking rate (prv. yr)	Stocking rate (cur. yr)	Dist. to road	Dist. to oil pad	Edge density	Ag
Stocking rate (cur. yr)	0.32					
Dist. to road	-0.03	-0.06				
Dist. to oil pad	0.03	-0.12	-0.33			
Edge density (75 m)	0.08	0.11	-0.03	0.11		
Ag (1,300 m)	0.08	0.03	-0.51	0.64	0.21	
Precip	-0.04	-0.06	0.01	0.01	-0.03	0.00

Table D2. Model selection results for Andersen-Gill models evaluating the relationship of edge density measured at different buffer lengths to mortality risk of female sharp-tailed grouse during the breeding season in eastern Montana and western North Dakota in 2016–2018.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. w_i	LL
75 m	1	509.36	0.00	0.20	0.20	-253.68
Null	1	509.36	0.01	0.20	0.39	-254.68
125 m	1	510.62	1.26	0.10	0.50	-254.31
30 m	1	510.69	1.33	0.10	0.60	-254.34
200 m	1	510.72	1.36	0.10	0.70	-254.36
500 m	1	511.18	1.82	0.08	0.78	-254.59
1300 m	1	511.31	1.95	0.07	0.85	-254.65
750 m	1	511.31	1.95	0.07	0.93	-254.66
1000 m	1	511.36	2.00	0.07	1.00	-254.68

Table D3. Model selection results for Andersen-Gill models evaluating the relationship of the proportion cropland measured at different buffer lengths to mortality risk of female sharp-tailed grouse during the breeding season in eastern Montana and western North Dakota in 2016–2018.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. w_i	LL
1300 m	1	509.28	0.00	0.18	0.18	-253.64
null	0	509.36	0.09	0.18	0.36	-254.68
1000 m	1	509.73	0.45	0.15	0.50	-253.86

30 m	1	510.36	1.08	0.11	0.61	-254.18
75 m	1	510.63	1.35	0.09	0.70	-254.31
750 m	1	510.73	1.45	0.09	0.79	-254.36
125 m	1	511.04	1.76	0.08	0.87	-254.52
200 m	1	511.32	2.05	0.07	0.94	-254.66
500 m	1	511.36	2.08	0.06	1.00	-254.68

Table D4. Preliminary model selection results for Andersen-Gill models evaluating the relationship between single variables representing habitat and inherent risk factors and the mortality risk of female sharp-tailed grouse during the breeding season in eastern Montana and western North Dakota in 2016–2018.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. w_i	LL
Ag	1	509.28	0.00	0.18	0.18	-253.64
Edge density	1	509.36	0.08	0.17	0.35	-253.68
Brood-rearing	1	509.36	0.08	0.17	0.52	-253.68
Null	1	509.36	0.09	0.17	0.69	-254.68
Precip	1	510.45	1.17	0.10	0.79	-254.22
Nesting	1	510.74	1.47	0.09	0.87	-254.37
Dist. to oil pad	1	511.31	2.03	0.06	0.94	-254.65
Dist. to road	1	511.36	2.08	0.06	1.00	-254.68

APPENDIX E

SIMULATION RESULTS EVALUATING THE SAMPLING INTENSITY
NECESSARY WHEN DEFINING A USED:AVAILABLE RATIO

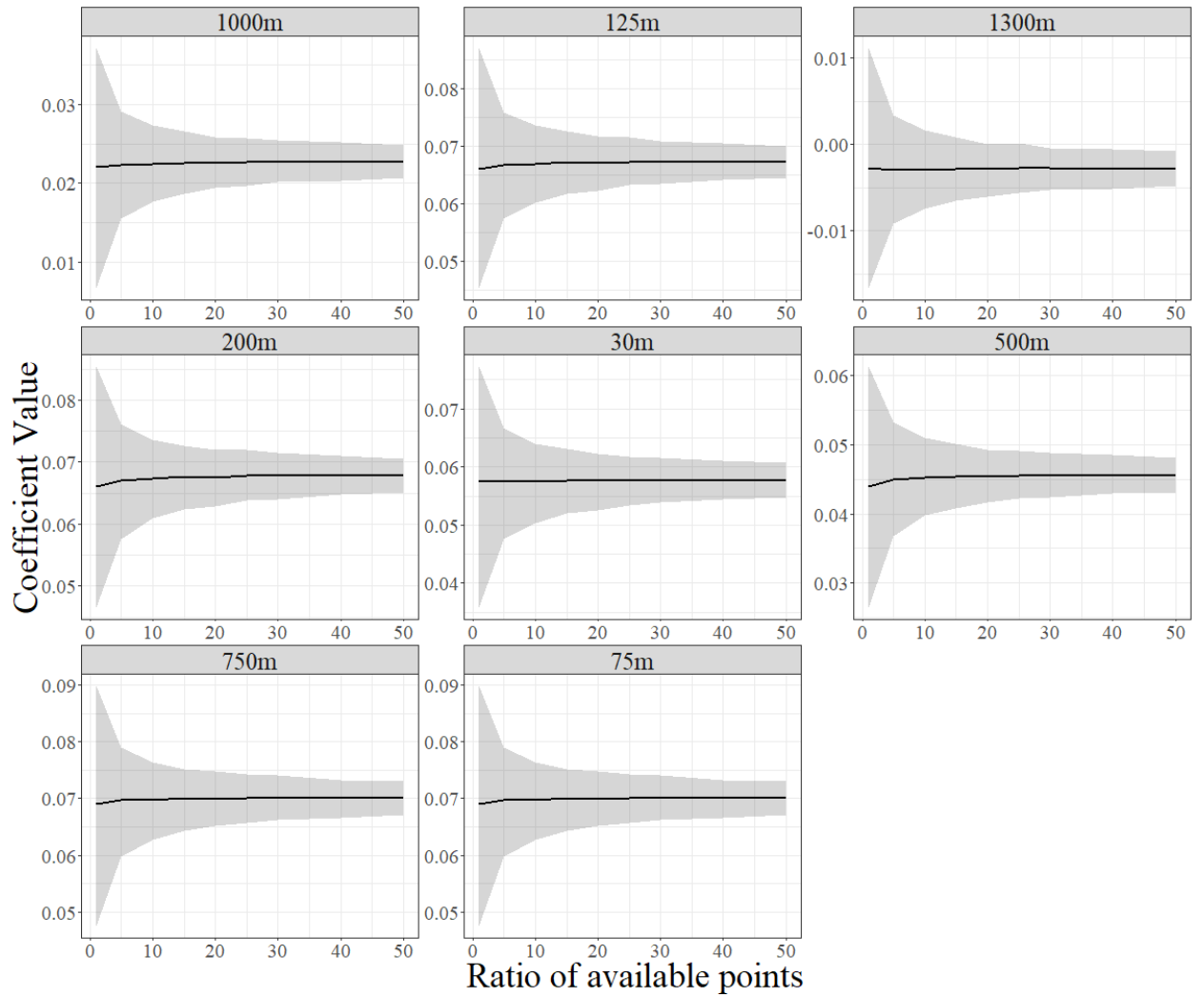


Figure E1. Simulation results evaluating the number of available points necessary for convergence of the proportion grassland measured at different buffer distances.

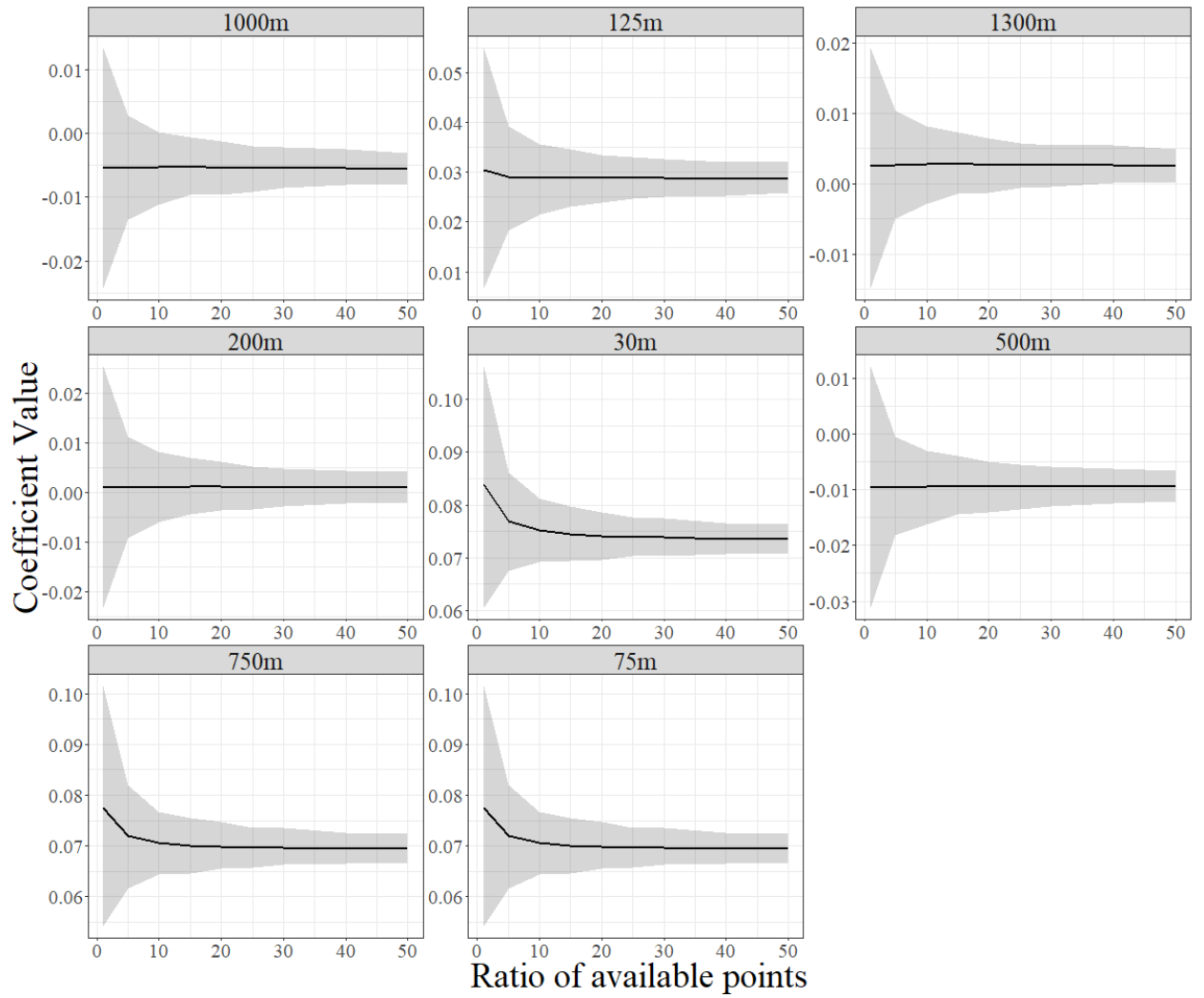


Figure E2. Simulation results evaluating the number of available points necessary for convergence of the proportion wooded draws measured at different buffer distances.

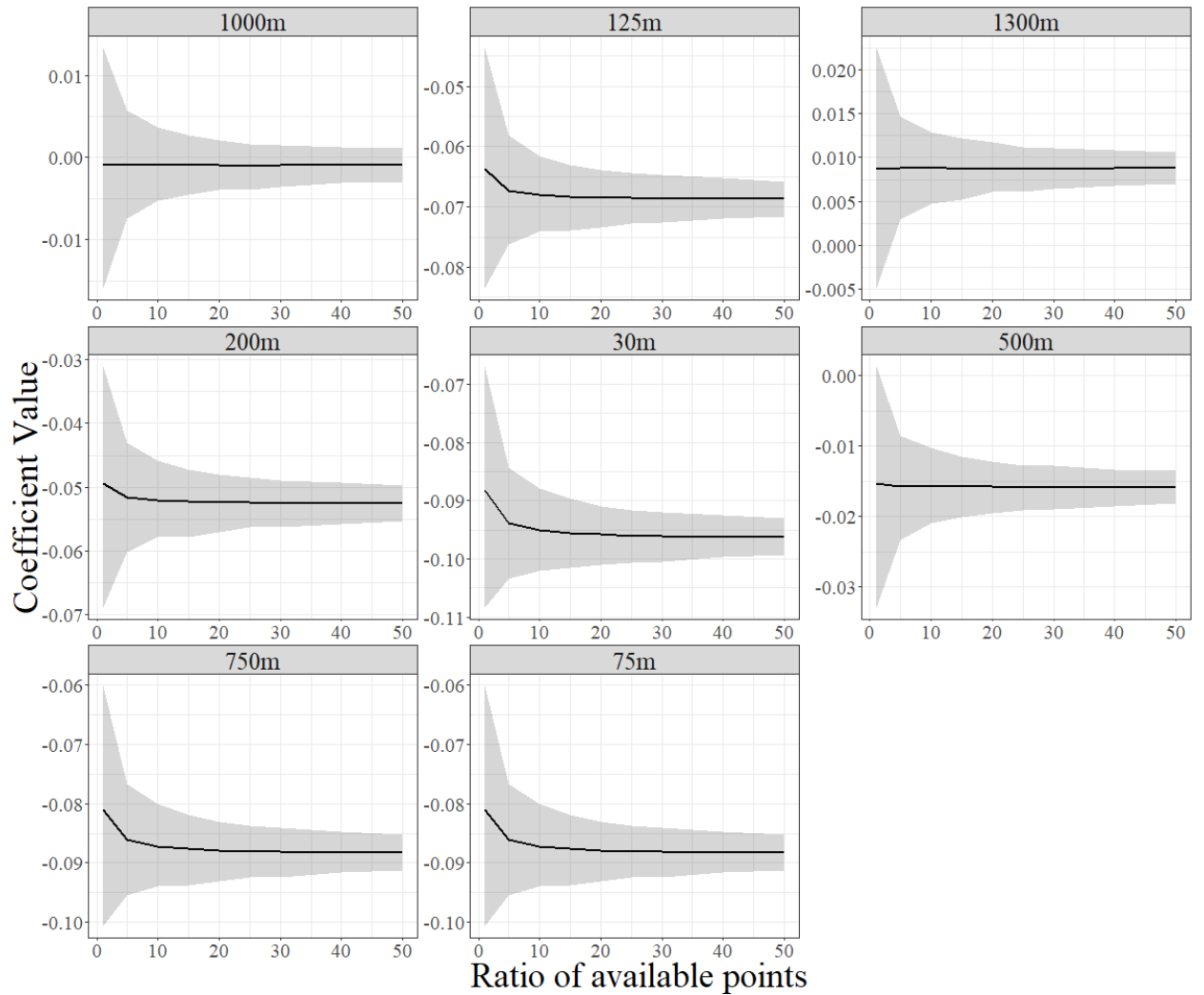


Figure E3. Simulation results evaluating the number of available points necessary for convergence of the proportion cropland measured at different buffer distances.

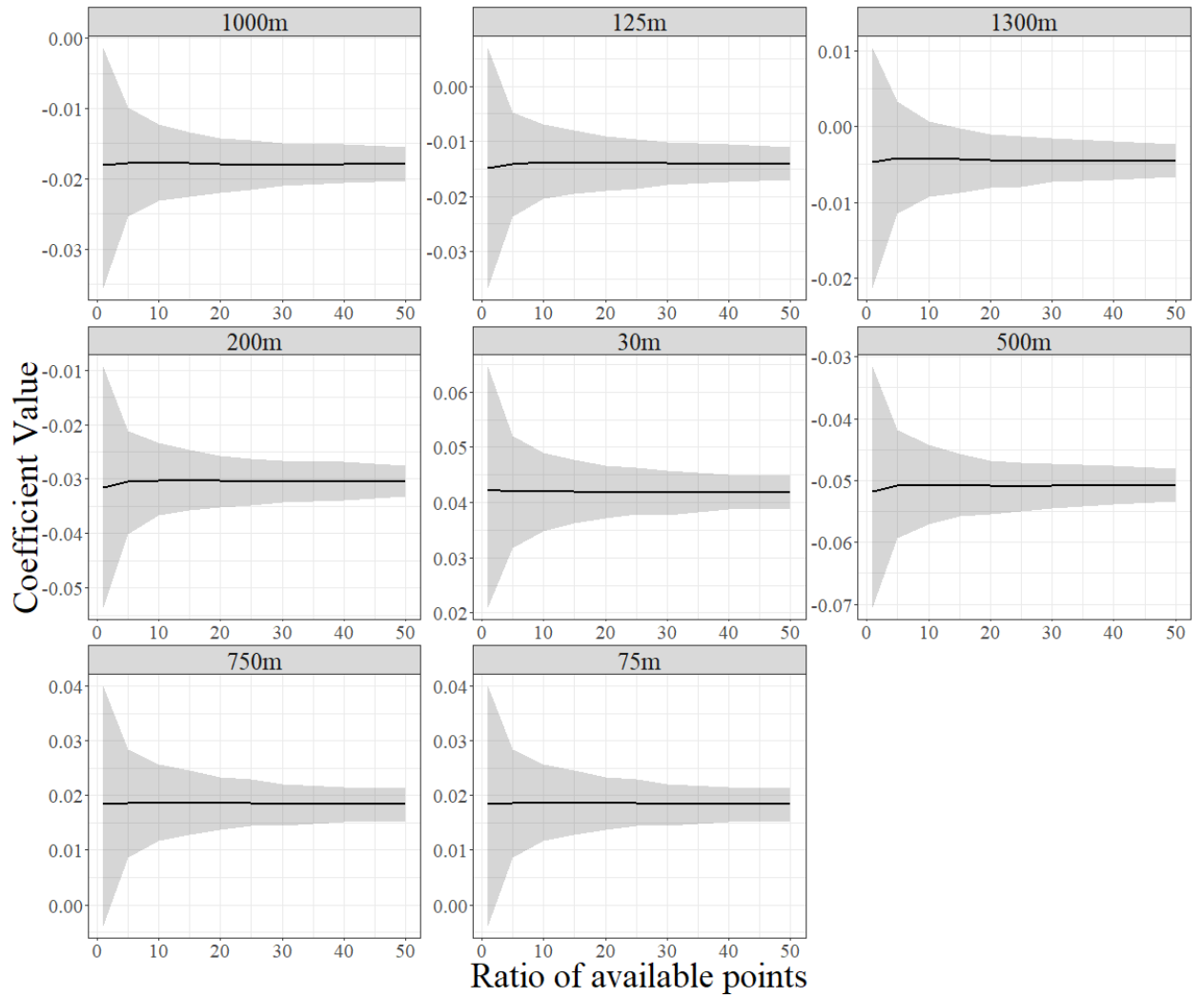


Figure E4. Simulation results evaluating the number of available points necessary for convergence of the edge density measured at different buffer distances.

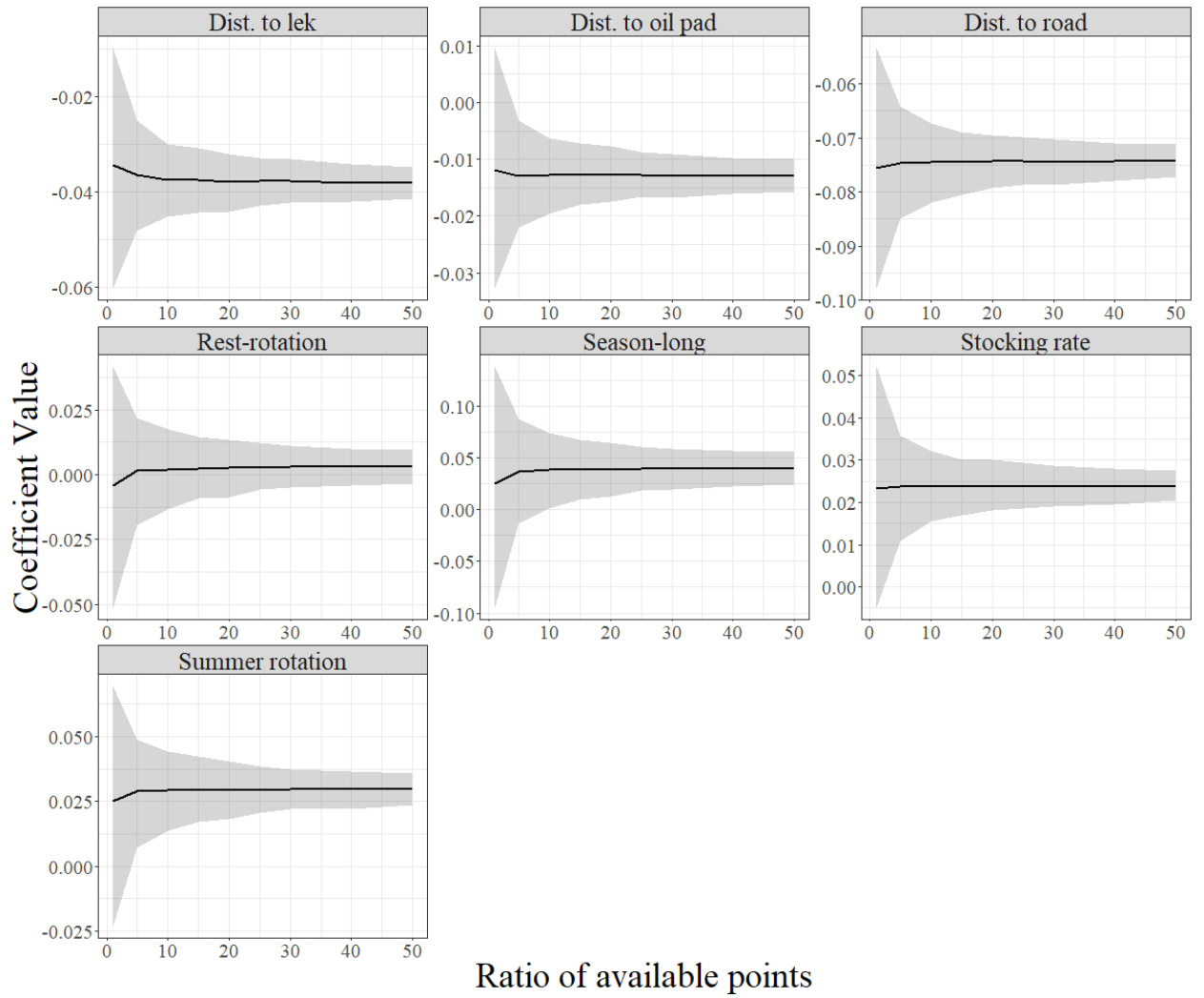


Figure E5. Simulation results evaluating the number of available points necessary for convergence of variables measured at a single scale.

APPENDIX F

RELATIONSHIP BETWEEN SAMPLING INTENSITY AND HOME RANGE SIZE

Table F1. Support for candidate models predicting the relationship between the number of locations per female and home range size of female sharp-tailed grouse during the breeding seasons of 2016–2018. 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
Null	2	2166.80	0.00	0.45	0.45	-1081.36
# Locations	3	2167.23	0.44	0.36	0.81	-1080.53
# Locations + # Locations ²	4	2168.53	1.74	0.19	1.00	-1080.12

APPENDIX G

SUPPORTING INFORMATION FOR THE THIRD-ORDER HABITAT SELECTION
ANALYSIS

Table G1. Support for models predicting the spatial grain of proportion grassland that best predicts sharp-tailed grouse habitat selection. The leave-one-out information criterion (LOOIC), the SE of LOOIC, DIC values, Δ DIC values, and coefficient estimates (β) and upper (UCI) and lower confidence intervals (LCI) are reported.

Grain	LOOIC	SE	DIC	ΔDIC	β	LCI	UCI
1300m	808.42	12.28	62805.31	0.00	0.27	0.11	0.43
750m	807.97	12.52	62842.46	37.15	0.37	0.23	0.51
1000m	808.74	12.44	62853.75	48.44	0.34	0.20	0.49
500m	807.95	12.62	62920.91	115.59	0.31	0.20	0.43
200m	808.24	12.73	62923.00	117.69	0.25	0.16	0.35
125m	808.75	12.75	62996.12	190.81	0.22	0.14	0.31
30m	808.10	10.74	63017.46	212.15	0.15	0.08	0.22
75m	808.90	12.75	63030.43	225.11	0.18	0.11	0.26

Table G2. Support for models predicting the spatial grain of proportion wooded draws that best predicts sharp-tailed grouse habitat selection. The leave-one-out information criterion (LOOIC), the SE of LOOIC, DIC values, Δ DIC values, and coefficient estimates (β) and upper (UCI) and lower confidence intervals (LCI) are reported.

Grain	LOOIC	SE	DIC	ΔDIC	β	LCI	UCI
1300m	644.45	9.91	62402.51	0.00	-0.05	-0.19	0.09
1000m	643.42	9.92	62586.77	184.26	-0.06	-0.18	0.05
500m	643.85	9.94	62664.49	261.98	-0.02	-0.10	0.05
750m	643.48	9.97	62747.64	345.13	-0.01	-0.09	0.07
200m	643.15	9.94	62873.43	470.92	-0.08	-0.14	-0.01
125m	643.26	10.12	63010.50	607.99	-0.05	-0.11	0.00
75m	643.56	10.41	63152.05	749.54	0.00	-0.05	0.04
30m	643.17	10.41	63258.08	855.57	0.02	-0.02	0.06

Table G3. Support for models predicting the spatial grain of proportion cropland that best predicts sharp-tailed grouse habitat selection. The leave-one-out information criterion (LOOIC), the SE of LOOIC, DIC values, Δ DIC values, and coefficient estimates (β) and upper (UCI) and lower confidence intervals (LCI) are reported.

Grain	LOOIC	SE	DIC	ΔDIC	β	LCI	UCI
500m	643.33	9.95	63206.24	0.00	-0.37	-0.50	-0.26
200m	644.06	10.17	63209.34	3.11	-0.37	-0.48	-0.25
125m	643.22	10.28	63215.67	9.43	-0.35	-0.47	-0.24
1300m	644.09	9.95	63216.24	10.01	-0.33	-0.47	-0.21
75m	643.62	10.31	63235.30	29.06	-0.33	-0.43	-0.23

30m	643.82	10.35	63235.63	29.40	-0.32	-0.42	-0.23
750m	644.07	9.97	63250.02	43.78	-0.30	-0.42	-0.19
1000m	643.36	9.91	63252.53	46.30	-0.29	-0.40	-0.20

Table G4. Support for models predicting the spatial grain of edge density that best predicts sharp-tailed grouse habitat selection. The leave-one-out information criterion (LOOIC), the SE of LOOIC, DIC values, Δ DIC values, and coefficient estimates (β) and upper (UCI) and lower confidence intervals (LCI) are reported.

Grain	LOOIC	SE	DIC	ΔDIC	β	LCI	UCI
1000m	872.36	55.65	62721.80	0.00	-0.06	-0.16	0.03
125m	844.07	52.86	62826.72	104.91	-0.08	-0.14	-0.01
1300m	874.96	57.13	62760.03	38.22	-0.03	-0.13	0.08
200m	844.93	53.16	62673.41	-48.39	-0.07	-0.15	0.00
30m	834.40	53.11	62875.77	153.96	-0.05	-0.11	0.01
500m	855.49	54.34	62632.73	-89.07	-0.07	-0.16	0.02
750m	874.36	55.40	62614.43	-107.38	-0.08	-0.18	0.02
75m	837.90	52.94	62879.39	157.59	-0.06	-0.12	0.00

Table G5. Multicollinearity results for management and landscape variables in the full third order resource selection analysis.

	% Grassland	% Wooded draws	% Ag	Edge density	Dist. to oil pad	Dist. to road	Stocking rate (current)
% Wooded draws	-0.54						
% Ag	-0.72	0.17					
Edge density	-0.64	0.62	0.25				
Dist. to oil pad	-0.55	0.21	0.48	0.11			
Dist. to road	0.48	-0.19	-0.36	-0.06	-0.35		
Stocking rate (current)	-0.08	-0.02	-0.05	0.08	-0.02	-0.01	
Stocking rate (previous)	0.11	-0.07	-0.11	-0.09	-0.14	0.11	0.47