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Greater Sage-Grouse Brood Responses to Livestock Grazing in Sagebrush Rangelands

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GREATER SAGE-GROUSE BROOD RESPONSES TO LIVESTOCK

GRAZING IN SAGEBRUSH RANGELANDS

by

Hailey Peatross Wayment

A thesis submitted in partial fulfillment
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ABSTRACT

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by

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Utah State University, 2022

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The role of livestock grazing in managing wildlife and their habitats on western rangelands has been long-debated by public land stakeholders, local communities, landowners, livestock producers, and wildlife managers. The controversial nature of this debate stems from limited, and often conflicting data regarding the effect grazing has on habitat vegetation structure and wildlife communities. At the core of this debate is the greater sage-grouse (*Centrocercus urophasianus*, sage-grouse), a keystone sagebrush (*Artemisia* spp.) rangeland obligate species, that experienced population declines primarily attributed to habitat loss and degradation. Although range wide conservation efforts have stabilized local populations, the fact that over 80% of the range is grazed by livestock may provide the greatest opportunity to develop a rangeland management strategy. In Utah, research demonstrated that sage-grouse inhabiting privately-owned sagebrush rangelands managed under deferred-rest rotation grazing systems had higher nest success than sage-grouse inhabiting areas managed under a combined deferred rotational and season-long grazing regime.

The research was conducted on two study sites within Rich County. The first study site was Deseret Land and Livestock (DLL) and the second study site was the Three Creeks Allotment (3C). We analyzed brood habitat selection of sage-grouse in response to vegetation dynamics and the interactions with livestock grazing to determine whether the relationship between sage-grouse and cattle was competitive or facilitative.

This research adds new information to the literature pertaining to the knowledge gap between livestock grazing and whether it is facilitative or competitive with brooding sage-grouse. Our results suggest that the relationship between livestock and sage-grouse might be competitive on the short term but facilitative over longer time scales. These findings indicated that deferred-rest rotational grazing practices may allow for spatio-temporal segregation between sage-grouse and livestock thus enhancing the capacity for sage-grouse to optimize the exploitation of available forage while avoiding direct contact with livestock. Further, our results suggest that livestock grazing could have carry-over effects on vegetation dynamics that may benefit sage-grouse in subsequent seasons, although we did not test this directly. More research is needed to understand the effects of livestock grazing across multiple growing seasons.

(74 pages)

PUBLIC ABSTRACT

Greater Sage-grouse Brood Responses to Livestock Grazing In Sagebrush Rangelands

Hailey P. Wayment

The distribution and abundance of the greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) have declined in the last 60 years. Range contractions and population declines have been attributed to loss and fragmentation of their sagebrush (*Artemisia* spp.) habitats. Grazing by livestock remains the predominant anthropogenic land-use across sagebrush ecosystems in North America, occurring on 87% of remaining sage-grouse habitat. Most of the peer-reviewed literature reports the potential for negative impacts of sagebrush reduction treatments, to increase livestock forage, on sage-grouse habitat. However, few studies have linked livestock grazing at the landscape level to vital rates (e.g., nest initiation rates, nest success, brood movements, and brood success) for ground-nesting birds such as sage-grouse.

We analyzed brood habitat selection of sage-grouse in response to vegetation dynamics and, where possible (DLL), in interaction with livestock grazing to determine whether the relationship between sage-grouse and cattle is competitive or facilitative.

This research adds new information to the literature pertaining to the knowledge gap between livestock grazing and whether it is facilitative or competitive with brooding sage-grouse. Our results suggest that the relationship between livestock and sage-grouse might be competitive on the short term but facilitative over longer time scales. These findings indicate that deferred-rest rotational grazing practices may allow for spatio-temporal segregation, enhancing the capacity for sage-grouse to optimize the exploitation

of available forage while avoiding direct contact with livestock. Further, our results suggest that livestock grazing could have carry-over effects on vegetation dynamics that may benefit sage-grouse in subsequent seasons, although we did not test this directly; more research is needed to understand the effects of livestock grazing across multiple growing seasons.

DEDICATION

This thesis is dedicated to my grandfather, James E. Carter, who passed away June 20, 2018. Grandpa Jim was the cultivator of my interests in the outdoors since I was old enough to walk. As an avid outdoorsman, naturalist, and of course fisherman, Grandpa Jim was the perfect example of how to appreciate and take care of the beautiful world around us. Grandpa Jim has been by my side through the good and bad times of this project, he has gently pushed me to keep going and see it through. This is as much my thesis as it is his. Thank you, Grandpa, I love and miss you.

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Hailey P. Wayment

CONTENTS

LIST OF FIGURES

Page

INTRODUCTION AND HISTORY

Range-wide Population Status

Greater sage-grouse (*Centrocercus urophasianus*, sage-grouse) are restricted to the sagebrush (*Artemisia* spp.) rangelands of western North America, and are considered an important indicator species of that ecosystem. Currently, populations exist in only 11 states; Washington, Oregon, California, Nevada, Utah, Idaho, Montana, Wyoming, Colorado, North and South Dakota, and 2 Canadian provinces; Alberta and Saskatchewan (Schroeder et al. 2004).

The distribution and abundance of sage-grouse have declined in the last 60 years (Connelly et al 2004). This decline has been primarily attributed to loss and fragmentation of their sagebrush habitats (Connelly and Braun 1997, Knick et al. 2003, Schroeder et al. 2004, Garton et al. 2011), on which sage-grouse and other sagebrush-obligate species depend. Increased anthropogenic activities such as; introduction of invasive species, development of sagebrush communities for agriculture and urban development, and poor livestock management, have been identified as detrimental to sage-grouse (Connelly et al. 2004, Schroeder et al. 2004). However, little research has addressed the role of livestock management in relation to these declines. As a result, these anthropogenic activities have disrupted forage and cover areas, and have been implicated in loss of breeding, brood rearing, and important wintering habitat, which leads to sporadic movements and increased predation risks for sage-grouse (Coates and Delehanty 2010).

Because of this decline, a species status review was completed by the U.S. Fish and Wildlife Service (USFWS) in 2005. The USFWS determined that the sage-grouse was not warranted for protection under the Endangered Species Act of 1973 (USFWS 2015). In 2010, the USFWS identified sage-grouse as a candidate species for protection under the Endangered Species Act (USFWS 2010), listing concerns such as habitat loss and inadequate regulations (USFWS 2010). This decision prompted state and federal agencies, industry, private landowners, and other stakeholders to initiate unprecedented efforts to mitigate the species' range-wide conservation threats. Collectively, these efforts resulted in the 2015 decision by USFWS that the species no longer warranted consideration for ESA protection (USFWS 2015, Western Association of Fish and Wildlife Agencies [WAFWA] 2015).

Sage-grouse in Utah

Utah supports an estimated 6.8% of the global sage-grouse population (WAFWA 2015). It is thought that historically, sage-grouse were present in all 29 Utah counties, based on the historical distribution of sagebrush (*Artemisia* spp.), pioneer records, and museum specimens (Beck et al. 2003). Currently, Uintah, Rich, Wayne, western Box Elder, and Garfield counties contain the largest populations in the state. Estimates show that sage-grouse occupy about 41% of their historical range in Utah (Beck et al. 2003**)** and now only currently exist in 26 Utah counties (Utah Division of Wildlife Resources [UDWR] 2002). In 2019 Utah's Greater Sage-grouse Conservation Strategy (Utah Plan) was published by the Utah Public Land Policy Coordination Office (PLPCO 2019) and Governor Gary R. Herbert signed an Executive Order to implement it. In 2020, UDWR developed Utah' first statewide sage-grouse comprehensive management plan.

The scientific foundation for the 2019 Utah Plan was based upon >20 years of research completed by Utah State University (USU), Brigham Young University (BYU), UDWR, and range wide partners (Messmer 2018). The Utah Plan outlines goals, and objectives for sage-grouse populations and their conservation in Utah. To help accomplish these goals the state of Utah established 11 sage-grouse management areas (SGMAs) which encompass over 300,000 ha of viable habitat that encompasses 94% of Utah's sage-grouse population (Dahlgren et al. 2016, PLPCO 2019).

The SGMA boundaries include seasonal habitats and identify areas where conservation efforts potentially have the greatest value (Dahlgren et al. 2016). These data are housed by the USU Community-Based Conservation Program and represents the most comprehensive local population habitat-use and vital rate dataset range-wide with over 800,000 sage-grouse locations (Picardi 2021). This database provided the scientific information that guided the goals and objectives for the Utah plan and directs how Utah manages sage-grouse habitat and populations (PLPCO 2019).

Utah exhibits unique topography and geography characterized by mountainous terrain, the Great Basin valleys and the canyons of the Colorado Plateau (West 1983). Because of these characteristics, sage-grouse habitat is found in natural fragments, islands in the Colorado Plateau, or large intact blocks (Perkins 2010, Dahlgren et al. 2016). Sage-grouse populations can vary as some populations are considered non-migratory and other are migratory, potentially moving more than 50 km between seasonal habitats (Connelly et al. 2000). Due to this variation, SGMAs became the focus of habitat improvements and restoration as they contained the greatest potential benefit for populations of sage-grouse in Utah (Dahlgren et al. 2016). Currently private lands contain 40.5% of sage-grouse populations, Bureau of Land Management (BLM) lands at 34.4%, U.S. Forest Service (USFS) managed land at 9.7%, and Utah state lands at 9.5%. The remaining habitat falls under School and Institutional Trust Land Administration, Division of Parks and Recreation, UDWR and Ute Tribal lands (UDWR 2009). Because almost half of the sage-grouse in Utah occupy private lands, land owners and federal and state agencies had to collaborate to implement habitat improvements and other projects to conserve and increase populations of sage-grouse throughout the state. Since 2006 over 200,000 ha of sage-grouse habitat has been enhanced or restored as a result of this collaborative effort (PLPCO 2019).

Rich County Population

One of the state's largest sage-grouse populations is located in northeastern Utah in Rich County, which falls under the Rich-Morgan-Summit SGMA and the southwestern portion of the Wyoming Basin Sage-grouse Management Zone II (Beck et al. 2003, Knick and Connelly 2011, PLPCO 2019). The UDWR has been monitoring sage-grouse lek sites in Rich County since 1959 (Rich County 2006). Since then, the number of known and monitored leks has increased from less than 10 to 46 active leks (Rich County 2006). Rich County encompasses 267,808 ha most of which is private land. Other land managers include the USFS, BLM, and SITLA. This population is part of a metapopulation that includes parts of eastern Idaho and western Wyoming (Dettenmaier et al. 2012).

Deseret Land and Livestock (DLL) is an 80,600 ha privately-owned ranch in southern Rich County, that abuts 6,300 ha of BLM lands. Previous research conducted on DLL indicated that sage-grouse show greater lek fidelity and higher productivity when deferred-rest rotation grazing and habitat treatments were completed (Dahlgren et al. 2015b, Danvir et al 2005). Many of the privately-owned ranches in Rich County are seasonally important to more wildlife species than just sage-grouse. History has shown that when public and privately-owned rangelands are managed properly, habitat and wildlife species are positively affected (Thomas and Gripne 2002). Danvir (2002) expressed the importance of research being conducted on private lands and programs that provide private landowners the training, and economic assistance to preserve and enhance wildlife ecosystems.

Little was known about sage-grouse habitat use until Homer (1991) investigated winter habitat by following radio-collared sage-grouse. He concluded that Wyoming big sagebrush was the dominate shrub for wintering sage-grouse. Hunnicuttt (1992) expanded the seasonal mapping started by Homer (1991) to include areas used for nesting and brood rearing. Sage-grouse females with broods required a greater mosaic of habitat then compared to males or females without broods (Hunnicutt 1992). This research, along with others has shown a positive population trend since 1959 (Danvir 2002, Dahlgren et al. 2015a), but this has also been attributed to increased monitoring efforts and the discovery of more leks (Rich County 2006, Messmer 2018).

Sage-grouse populations in Rich County seem to be driven mainly by habitat and weather (Danvir 2002, Dahlgren et al. 2015b). Rich County experiences harsh winters with deep snow and hot dry summers. This affects sage-grouse as they express fidelity to their seasonal habitats and rely on sagebrush for cover and food in the winter, and forbs and insects in the summer (Connelly et al. 2000, Dahlgren et al. 2015b, Danvir 2002). Research has suggested that deep snow and dry summers can limit the reproductive rate and survival of sage-grouse. (Dahlgren et al. 2015b, Danvir 2002)

GREATER SAGE-GROUSE ECOLOGY

The sage-grouse is the largest grouse species in North America. Sage-grouse follow a polyandrous mating system where males compete each spring for breeding opportunities (Patterson 1952). Male sage-grouse are known for their extravagant strutting behavior in the early morning hours on leks, with their tails fanned out, inflating and deflating two yellow throat sacs, and sometimes physical wing smashing fights. Males weigh almost twice as much as females at 3.2 kg and 1.5 kg respectively (Autenrieth 1981). Sage-grouse are known for their dependence on the shrub species sagebrush, iconically found in the West. Sage-grouse rely on sagebrush for protection, nesting, and as a food source (Connelly et al. 2011b). As with many wildlife species sage-grouse have varying habitat requirements as seasons change and they tend to exhibit a high fidelity to the seasonal ranges they use, best exemplified by repeated use of nest sites by hens (Connelly et al. 2011b).

Breeding

Breeding for sage-grouse takes place on designated strutting grounds known as “leks”. In early March males start congregating and performing courtship displays. For the Northwestern part of Utah lekking occurs from early March through the first week of June (Box Elder Adaptive Resource Management Local Working Group (BARM 2007). Lekking areas are characterized by sparse short vegetation or bare ground, including bare ridges and roads (Patterson 1952, Connelly et al. 1981). Leks generally occur near areas suitable for nesting (Connelly et al. 2000). The same lekking locations are used year after year, but can also shift if there is a disturbance such as deep snow cover, site disturbance, or other physical changes to the area (Connelly et al. 2011a). Lekking areas are also often formed opportunistically in areas where female presence is high (Gibson 1992, Connelly et al. 2000). Typically, there is a dominant male on the lek who develops a territory and defends it. This male will mate with the majority of the females (Wiley 1973). Eng (1963) and Jenni and Hartlzer (1978) suggested that about half of the males in the population congregate on the lek shortly after the lekking season begins. Female presence at the leks typically lasts up to two weeks, peaking from late March to early April (Eng 1963, Connelly et al. 2011a). It is not uncommon for females to visit multiple leks throughout the breeding season (Schroeder and Robb 2003). Peak male attendance occurs a few weeks after the female peak as sub-dominant males such as yearlings are admitted on the lek (Eng 1963, Connelly et al. 2011a). Timing of peak lek attendance may shift between a matter of days to weeks depending on current weather conditions (Schroeder 1997, Connelly et al. 2011a). Because sage-grouse have a high fidelity to lekking areas, populations can be monitored by counting the number of males present on each lek. (Connelly et al. 2003, Connelly and Schroeder 2007).

Nesting

Approximately 10 days after female lek attendance peaks, about 78% of females begin nest initiation (Wallestad 1975, Schroeder 1997, Connelly et al. 2011a). Sage-grouse have been found to have lower reproductive rates but higher survival rates in comparison to other upland game bird species (Connelly and Braun 1997). Typically, nests are found within 5 km of a lek but this value ranges from 1 to 20 km (Braun et al. 1977, Holloran et al. 2005, Connelly et al. 2000, Dahlgren et al. 2016, Picardi et al. 2020). Sage-grouse nests are generally located under the tallest sagebrush plant in a shrub stand (Wallestad and Pyrah 1974, Apa 1998). Gibson et al. (2016) suggested that nesting habitat was based more on its qualities as brood rearing habitat then quality nesting areas. Nesting areas generally have a total canopy cover between 15-30%, with most nests being established under shrubs with height ranges from 29 to 80 cm (Connelly et al. 2000, Apa 1998). Sage-grouse that nest under sagebrush have been found to have a higher nest success than sage-grouse that nest under other plant species, generally due to a decrease in canopy cover (Connelly et al. 1991). Adult female sage-grouse were recorded in one study as having a higher nest success rate than yearling females though it is highly variable (Wallestad and Pyrah 1974, Connelly et al. 1993, Schroeder 1997).

During the nest initiation period, females deposit one egg in the nest every day and a half (Schroeder et al. 1999). A typical clutch size will range between 6 to 10 eggs (Dahlgren 2006, Knerr 2007). Incubation begins once all of the eggs are laid and can last between 25-29 days (Patterson 1952, Connelly et al. 2011a). Nest success can range from 15-85%, with most of this variation explained by habitat quality, female age, and predator abundance (Connelly et al. 2011a).

Female sage-grouse generally exhibit a high fidelity to successful nest sites (Berry and Eng 1985, Fischer et al. 1993, Holloran et al. 2005, Schroeder and Robb 2003). If a nest failure occurs a female may re-nest laying a smaller clutch than the previous attempt, with older adults being more likely to re-nest (Schroeder 1997, Connelly et al. 2011a). Conversely, females that had a failed nest attempt(s) will nest in a new area. (Schroeder and Robb 2003).

Predation is one of the most common reasons for sage-grouse nest failure. Vegetation structure with sagebrush stands 40-80 cm in height seem to reduce predation.

(Gregg et al. 1994, Schroeder and Baydack 2001). Vegetation diversity is crucial as it may provide scent, visual, and physical obstructions for predators, and better conceal nests (DeLong et al. 1995, Connelly et al. 1991). Common nest predators include badger (*Taxidea taxus*), coyote (*Canis latrans*), and common raven (*Corvus corax*). Common adult sage-grouse predators are golden eagle (*Aquila chrysaetos*), red-tailed hawk (*Buteo jamaicensis*), Swainson's hawk (*Buteo regalis*), and northern harrier (*Circus cyaneus*) (Schroeder and Baydack 2001).

Brood-rearing

Sage-grouse chicks are precocial, being able to walk and move around immediately after hatching. Shortly after hatching the female will move her brood away from the immediate nest area, but will remain within 3 km of the nest site for the first 2-3 weeks (Berry and Eng 1985). This time period is when chicks face the highest risk of death (Gregg et al. 2007). Movement away from the nest has been found to be variable depending on the habitat structure and food availability (Klebenow 1969, Peterson 1970, Wallestad 1971, Drut et al. 1994, Connelly et al. 2000).

Brood-rearing is often divided into early and late periods. The early period is closely associated with nesting habitat, whereas late brood-rearing periods are associated with females moving to areas with a lower shrub canopy cover, but higher herbaceous understory (Connelly et al. 2000). Ideal brood-rearing areas contain a high abundance of insects and forbs (Apa 1998). Because of this, agricultural fields containing alfalfa tend to be used heavily by female sage-grouse and broods (Patterson 1952). Sage-grouse chicks are dependent on insects such as, beetles, ants, and grasshoppers, for their survival and growth (Patterson 1952, Johnson and Boyce 1990, Drut et al. 1994, Gregg and

Crawford 2009). Dahlgren (2006) found that chick survival was positively correlated with greater insect abundance. Apa (1998) reported that broods used areas that had twice as much forb cover than random locations. Sage-grouse do not contain a muscular gizzard like other bird species, meaning they can only digest soft plant and insect tissue (Patterson 1952). They contain a specialized digestive system which filters secondary compounds found in sagebrush, which can be toxic, from the fibrous plant material which contains nutrients (Clench and Mathias 1995).

Sage-grouse chicks can sustain short low flights at 2 weeks of age and strong flight by 5 weeks of age (Schreoder et al. 1999). After the first 2-4 weeks sage-grouse broods move to areas that are often higher in elevation and mesic habitat, this is generally in June and July (Gill 1965, Klebenow 1969, Connelly and Markham 1983, Fischer et al. 1996, Connelly et al. 2011a). Movement of sage-grouse broods from early to late brood-rearing sites varies greatly in distance, and late brooding sites generally contain greater sagebrush height (Connelly et al. 1988, Connelly et al. 2011b, Wallestad 1971, Dunn and Braun 1986). Survival of sage-grouse chicks is influenced by a variety of factors (Caudill et al. 2016), including weather (Rich 1985), food availability (Swenson 1986), and age of female (Gregg et al. 2006, Caudill et al. 2016). Brood-rearing continues until early fall, about 10-12 weeks after hatching, when sage-grouse begin to form flocks for winter (Schroeder et al. 1999).

Winter

As autumn moves into winter sage-grouse will begin moving to their wintering grounds. This usually occurs around November regardless of snow depth (Welch et al. 1990). During these winter months sage-grouse become entirely dependent on sagebrush not only for food but shelter and cover as well, which has to be accessible through the entire winter (Patterson 1952, Braun et al. 1977, Crawford et al. 2004). Preferred wintering habitats consist of medium to tall sagebrush with heights of > 25 cm and a canopy cover of 15% to 20% (Robertson 1991, Connelly et al. 2000). Research has indicated that sage-grouse select wintering sites based on topography and snow depth, and tend to prefer south facing slopes with <5% slope which receive more solar radiation in winter months, thereby exposing more sagebrush. (Robertson 1991, Beck 1977, Crawford et al. 2004). Due to increasing snow depth in the higher elevations, sage-grouse are generally found in low elevations during the winter months (Connelly et al. 2011b).

Sage-grouse have been found to actually gain weight over the winter subsisting completely on sagebrush. This substantiates the fact that sage-grouse are well adapted to consuming sagebrush and are not highly impacted by severe weather conditions unless the snow completely covers the sagebrush (Beck and Braun 1978, Hupp and Braun 1989). With sage-grouse foraging exclusively on sagebrush leaves in winter, big sagebrush (*A. tridentate*) is the preferred sagebrush species consumed by sage-grouse (Patterson 1952, Wallested 1975, Remington and Braun 1985, Welch et al. 1988, Robertson 1991). Other species used by sage-grouse if available include low sagebrush (*A. arbuscular*), black sagebrush (*A. nova*) (Dalke et al. 1963, Beck 1977), fringed sagebrush (*A. frigida*) (Wallestad 1975) and silver sagebrush (*A. cana*) (Aldridge 1998). Some populations of sage-grouse have been reported to prefer Wyoming big sagebrush (*A. t. wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) (Remington and Braun 1985, Meyers 1992, Welch et al. 1988).

Sage-grouse survival over the winter months is typically high due to the fact that weather has little impact on survival (Crawford et al. 2004, Connelly et al. 2011a). Though sage-grouse have a high fidelity to other seasonal areas, they seem to exhibit lower fidelity to their winter ranges. (Welch et al. 1990). Sage-grouse will partially or completely bury themselves in the snow, this offers cover and thermal protection from winter temperatures. (Rich County 2006). Researchers have reported an 86% survival rate of juveniles in moderate elevation and 64% at higher elevations (Beck et al. 2006). Hausleitner (2003) and Wik (2002) reported survival rates between 82%-100% and 85%-100% respectively. In contrast, Moynahan et al. (2006) documented negative impacts on sage-grouse winter survival when severe winter weather covered the sagebrush with snow.

SAGE-GROUSE HABITAT USE AND REPONSE TO MANAGEMENT

Connelly et al. (2000) published range-wide habitat guidelines for sage-grouse. In their paper they called for the delineation, protection, and restoration of habitats based on a scientific baseline to designate and manage critical habitats. They acknowledged that when baseline information is lacking, inconsistencies and problems may arise when applying those guidelines to habitats within an ecologically diverse landscape. Although all sage-grouse are considered sagebrush obligates, the species occupies a diversity of sagebrush communities from shrub-dominated semideserts in the southwest to more perennial grass-dominated sagebrush-steppe in the northeast portions of their distribution (Picardi et al. 2020).

Dahlgren et al. (2016) combined microsite habitat vegetation parameters from radiomarked sage-grouse nest and brood locations in Utah with state-wide spatially continuous vegetation, climatic, and elevation data to develop sage-grouse habitat guidelines that encompass the range of ecological and environmental variation across Utah. Their results provided relevant guidelines for the conservation of Utah's sage-grouse populations (PLPCO 2019). This approach may have application to the use of livestock grazing, the predominate land use in areas occupied by sage-grouse, to manage diverse western ecosystems to benefit other species that occupy diverse habitats and physiographic regions. Dettenmaier et al. (2017) argued that it may be inappropriate to apply the results of studies regarding Galliformes response to livestock grazing across ecosystems. The USFWS (2015) acknowledged this dilemma when they concluded that livestock grazing was not a range wide threat to sage-grouse species.

Over 50% of the earths terrestrial landscapes are considered rangelands (Sala et al. 2017). Briske et al. (2017) defined rangelands as uncultivated lands dominated by grasses, forbs, and shrubs that are suitable for grazing by livestock, habitat for wildlife, and provide humans with ecosystem services. However, improper grazing, such as over stocking or over grazing, by livestock has been implicated as a threat to wildlife conservation (Krausman et al. 2009, Robinson et al. 2019). The prairie grouse species that inhabit rangelands of North America are considered some of the most imperiled and at greatest risk to improper livestock grazing practices (Silvy and Hagen 2004).

Worldwide, many grouse species (Tetraonidae) require rangeland landscapes that exhibit diverse vegetation structure and composition to complete their life cycle. Habitat loss and degradation have been identified as the primary threat to some grouse (Storch 2007, 2015) and intense livestock grazing has been implicated as a conservation threat for 6 of the 7 grouse species that occupy rangeland habitats (The IUCN Red List of Species, 2015). The primary threats posed by livestock to ground nesting birds are displacement, poor habitat (low sagebrush cover, limited food availability), and disturbance across the landscape.

Dettenmaier et al. (2017) performed a meta-analysis of the published literature on grouse-livestock relationships and found an overall negative effect of livestock grazing on grouse populations. However, they concluded the reported indirect effects of livestock grazing on grouse species were inconclusive and more reflective of differences in the experimental designs and ecological sites. With a projected increase in demand for livestock products (Thornton 2010), better information will be required to mitigate the anthropogenic effects of livestock grazing on rangeland wildlife (Hovick et al. 2015).

The decline in sage-grouse populations across western North America has been primarily attributed to fragmentation and loss of their sagebrush habitats caused by increased human activities (Connelly and Braun 1997, Knick et al. 2003, Schroeder et al. 2004, Garton et al. 2011). Grazing by livestock is the predominant anthropogenic land use across sagebrush ecosystems in North America, occurring on 87% of remaining sage grouse habitat (Crawford et al. 2004, Knick and Connelly 2011, Dettenmaier et al. 2017).

The USFWS did not identify livestock grazing as a major species conservation threat for sage-grouse (USFWS 2015). Compared to other anthropogenic activities, the impacts of livestock grazing are more diffuse across the landscape (Knick et al. 2011, Boyd et al. 2014). However, the USFWS still identified improper livestock grazing as a potential local conservation threat for sage-grouse because of reported negative impacts associated with reductions of herbaceous cover required for nest concealment and brood nutrition (Gregg et al. 1994, Schroeder and Baydack 2001, Holloran et al. 2005, Hagen 2011, Dahlgren et al. 2015a, USFWS 2015). The hypothesized mechanism for these negative impacts is that cattle grazing depletes the herbaceous vegetation that sage-grouse depend on during brood-rearing via indirect competition. Alternatively, it is possible that the presence of cattle on the landscape could negatively impact sage-grouse by reducing access to otherwise profitable foraging areas if sage-grouse avoid cattle, thus effectively resulting in competitive exclusion. Neither of these mechanisms has been tested.

To date, the suspected negative effects of cattle grazing on sage-grouse are controversial. Smith et al. (2018) argued that the methods historically used by biologists to sample herbaceous cover at sage-grouse nest sites, particularly grass height, were biased. This bias may have contributed to inappropriate BLM and USFS management recommendations regarding the role of grass stubble height and livestock grazing to sage-grouse nest fate (BLM 2015, BLM 2018, Smith et al. 2018). Research reported in peer-reviewed literature demonstrated the potential for negative impacts of sagebrush reduction treatments to increase livestock forage on sage-grouse habitat (Beck and Mitchell 2000), but few studies have linked livestock grazing at the landscape level to vital rates for ground-nesting Tetraonidae such as the sage-grouse (Dettenmaier et al. 2017).

In stark contrast, there is some evidence of potential positive effects of livestock grazing on sage-grouse populations. Danvir et al. (2005) and Dahlgren et al. (2015a) reported that Utah sage-grouse populations responded positively (i.e., increased numbers of males counted on leks, and number of broods observed) to long-term (> 25 years) deferred-rest rotation grazing practices and sagebrush cover reduction treatments implemented on DLL. A potential mechanism through which livestock could benefit sage-grouse is by stimulating new plant growth and prolonging forage availability through time; this mechanism has not been tested with livestock, but recent literature has shown that bison grazing promotes vegetation growth in grasslands and extends the duration of the growing season (Geremia et al. 2019). Understanding potential effects, positive or negative, of livestock grazing on sage-grouse population is important to ensure land can be properly managed to facilitate coexistence of human activities with conservation objectives for species of concern

In 2011, Utah State University (USU) initiated research on DLL and adjacent BLM and USFS livestock grazing allotments, known as Three Creeks (3C), to determine if sage-grouse vital rates (i.e., nest and brood success and juvenile and adult survival) differed by study area, and if any of the observed differences were related to vegetation composition and structure (Dettenmaier and Messmer 2014, 2015, 2016). The research incorporated a Before-After Control-Impact study design where pre-treatment data collected on DLL and 3C were to be compared to data collected on the allotment after it was consolidated under a deferred-rest rotation system, which allows for growing-season rest (Payne 2011). However, the 3C consolidation was delayed until the BLM National Environmental Policy Act (NEPA) process requirement could be met. The consolidation decision was signed on April 24, 2018, and it will be fully implemented in 2022 (Payne 2018).

Given that it may take several years for a sage-grouse population to respond to management actions (Dahlgren et al. 2006, Dahlgren et al. 2016), the NEPA delay provided the partners with insights regarding the underlying mechanisms – why and how – livestock grazing may affect sage-grouse populations. Reported sage-grouse nest survival between 2012-2015 was higher on DLL (33%) than 3C's (17%; Dettenmaier 2018). Additionally, several habitat vegetation and landscape parameters demonstrably linked to sage-grouse nest survival; taller sagebrush, grass, and forb height, (Kaczor et al. 2011, Knick and Connelly 2011, Doherty et al. 2014, Dinkins et al. 2016) were also higher under DLL's deferred-rest rotation regime than 3C's regime, which combined deferred rotational with season-long grazing. A deferred-rest rotation regime is defined as a system where cattle are given access to specific pastures for fixed periods of time, while other pastures are rested, specifically during the growing season (Dahlgren et al. 2015a). Season-long grazing is defined as a system where a pasture or area is grazed for the duration of the growing season. Deferred rotational grazing is defined as a system where pastures are periodically left un-grazed for a given amount of years. On 3C, season-long and deferred rotation grazing both occurred depending on individual ownership within the allotment and were also inconsistently employed throughout the study period.

The Dettenmaier (2018) models supported lower rabbitbrush (*Ericameria nauseosa*) cover and higher estimates of the standardized precipitation-evapotranspiration index (SPEI; Vicente-Serrano et al. 2010) as driving nest survival rates. The SPEI is a climatic drought index that combines precipitation and temperature. A higher SPEI index typically equates to greater water stress. The DLL study area exhibited less rabbitbrush cover, and is on average warmer, and receives less rainfall than 3C.

Dettenmaier (2018) demonstrated the potential for high intensity management practices implemented in xeric (dry) sagebrush rangeland areas to benefit sage-grouse. However, he also identified the complexities in conducting research to answer fundamental questions regarding the role of livestock grazing in managing xeric sagebrush rangeland landscapes for multiple purposes. Grazing studies implemented to evaluate the effects on wildlife and their habitats, must account for these land use legacy effects when making comparisons between studies and drawing conclusions (Ripplinger et al. 2015, Dettenmaier et al. 2017). This is particularly relevant in cold, arid systems, as shorter growing seasons and chronic water limitations increase the time required for plant communities to recover from disturbance. Ripplinger et al. (2015) suggested that the legacy effects from historical land uses and management actions in our study area may persist well beyond 50 years.

GRAZING AND THE GREEN WAVE

The seasonal flush of nutrient rich vegetation that tracks the temperature-moisture optimum through time has become known as the "green wave" (van der Graaf et al. 2006, van Wijk et al. 2012). Merkle et al. (2016) found that five ungulate species (bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), moose (*Alces alces*) and bison (*Bison bison*)) indigenous to the Mountain West capitalized on this green wave by selecting patches that had high nutrient content relative to availability. They found that while bighorn sheep look for patches that have close escape routes, and mule deer and elk selected patches with fewer trees, and moose selected patches that were more mesic; all the species studied selected patches that had high nutrient content. Geremia et al. (2019) found that bison in Yellowstone National Park have a different effect upon the green wave than originally thought. Instead of tracking the green wave like other migratory grazers bison in fact modify the green wave in a way that their grazing patterns caused grassland to green up faster and for a longer duration. These authors concluded that large aggregate grazers can engineer plant phenology through grazing (Geremia et al. 2019).

Similarly, Stoner et al. (2016) found that mule deer synchronize birthing and movements to match the period between the start and peak of the growing season, thereby optimizing the balance between forage predictability and quality. Aikens et al. (2017) showed that migrating mule deer track the progression of the green wave by comparing the date marked mule deer visited a location with the date of peak green-up at that same location. Stoner et al. (2020) showed a similar tracking in regards to sage-grouse nest initiation dates in Utah. Female sage-grouse timed their nest initiation with peak green-up.

Aidley (1981) reported that for avian species, migration at any scale occurred in response to a birds need for food, shelter or breeding sites (Allen and Singh 2016). These fine scale, daily decisions, move animals across the landscape as they track resources, resulting in well-define seasonal migration patterns (Hopcraft et al. 2013). Examples of this include; blue grouse (*Dendragapus obscurus*) which make elevation migrations based on seasonal habitats (Cade and Hoffman 1993), the spring migration of white-fronted geese (*Anser albifrons albifons*) and bar-head geese (*A. indicus*) which is also closely tied to nutrient quality of vegetation (van Wijk et al. 2012), and research from Shariatinajafabadi et al. (2014) who followed marked barnacle geese (*Branta leucopsis*) on their spring migration and found that migratory movements were correlated to forage quality.

Collectively, these studies suggest that mammals and birds in seasonal environments are attuned to variation in forage availability and quality. Herbaceous vegetation is most palatable during early growth phases between the spring flush and the peak of the growing season, becoming progressively less digestible as plants desiccate (Hebblewhite et al. 2008). One potential effect of herbivory by large-bodied ruminants such as cattle (“roughage eaters” Hofmann 1989) is to prevent maturation of plant tissues through grazing (Turner et al. 1993). Although controversial, the literature suggests that stimulation of compensatory growth in plants is a function of the duration and intensity of grazing, given inherent edaphic and climatic conditions (Turner et al. 1993).

Holechek et al. (1982) reviewed grazing systems and concluded that wildlife could benefit from livestock grazing if adequate biomass for plant recovery is left un-grazed. The hypothesis that the strategic use of livestock grazing can stimulate production and extend nutritional value of grasses has been proposed by wildlife managers and livestock producers. This hypothesis remains largely untested (Dettenmaier et al. 2017).

To open up mature dense stands of sagebrush to promote forb and grass production in high elevation grasslands, DLL combined sagebrush treatments with a prescribed grazing framework (Dahlgren et al. 2015a). Nesting sage-grouse depend on forbs and insects during the incubation period, and newly hatched chicks are almost entirely dependent on these same food items until ~ 6 weeks of age (Dahlgren et al. 2015b). Preliminary data suggested that the increase in forbs and grasses following range treatments provided greater forage for livestock, but may have also improved sage-grouse brooding habitat (Danvir et al. 2005). Morris and Thompson (1998) also reported that invertebrate densities were higher in grazed grasslands in New Mexico. In southcentral Utah, Dahlgren (2009) reported that forb cover could be increased by late season grazing, resulting in increased use by sage-grouse. In northeastern Oklahoma and eastern Kansas traditional spring burning has been used to alter small patches in lieu of landscape scale burning. This alteration has changed the way that bison and cattle graze by concentrating on new growth that the burns promote. This has resulted in a more mosaic landscape to better meet the annual needs of greater prairie chickens (*Tympanuchus cupido*; Boyd et al. 2011). Thus, what remains to be determined, is whether the intensity and duration of grazing has facilitative or competitive relationships with sage-grouse (Monroe et al. 2017), especially during the critical brood rearing life phase.

We analyzed brood habitat selection of sage-grouse in response to vegetation dynamics and, where possible (DLL), an interaction with livestock grazing to determine whether the relationship between sage-grouse and cattle is competitive or facilitative. First, we hypothesized that sage-grouse would select for high-quality forage by selecting for intermediate values of biomass (usually associated with high palatability; Hebblewhite et al. 2008) both in DLL and 3C. Second, in DLL, we tested the hypothesis of a facilitative relationship between livestock and sage-grouse, according to which prescriptive grazing could promote rejuvenation of forage resources that support the needs of sage-grouse through the brood rearing period; under this hypothesis, we predicted that sage-grouse would select for recently grazed areas. Conversely, if the relationship between livestock and sage-grouse is competitive, we predicted sage-grouse would avoid recently grazed areas.

RESEARCH PURPOSE

The purpose of the study was to evaluate sage-grouse brood habitat-use and behavioral responses to livestock grazing. We monitored female sage-grouse that were fitted with either very high frequency collars (VHF) or global positioning system (GPS) rump-mounted transmitters from 2012-2020. We focused on female sage-grouse because they drive population growth (Caudill et al. 2014). Given the differences in grazing management practices between 3C and DLL, we hypothesized that sage-grouse brood-rearing habitat-use patterns would differ depending on the grazing strategy of the study area. If so, can the observed differences be explained by avoidance behavior or vegetation composition and structure that are the result of livestock grazing?

This project provides new information regarding sage-grouse behavioral responses to the presence of cattle. This research will guide the 3C consolidation to include subsequent management actions that may include additional land treatments to create more forage for livestock and food and cover for sage-grouse. Moreover, these efforts also provide new information regarding how livestock grazing can be used as a compensatory mitigation tool to offset the disturbances that may occur in sage-grouse habitats (Messmer 2013).

STUDY AREA

To test our questions, we capitalized on previous research conducted in Rich County, Utah, in the western United States. Rich County is located in northeastern Utah and constitutes the southwestern portion of the Wyoming Basin Sage-grouse Management Zone II (Knick and Connelly 2011), and falls under the Rich-Morgan-Summit Sage-grouse Management Area (SGMA, 1). Rich County encompasses 267,804 hectares of which 128,010 ha are private lands. The remaining lands are administered by the USFS, BLM, and School and Institutional Trust Lands Administration. The sage-grouse population inhabiting Rich County is connected to other populations of eastern Idaho and western Wyoming (Dettenmaier et al. 2012).

The research was conducted on two study sites within Rich County (Fig. 1). The DLL study site is a 86,900 ha privately-owned ranch comprised of roughly 80,600 ha of private lands and 6,300 ha of federal BLM lands located in the lower elevations. The DLL study area was managed as a cohesive unit, and in 1979 land managers moved to deferred-rest rotation grazing strategy which divided the landscape into multiple pastures, allowing some to rest during the growing season (Messmer 2013). Under this system, several large herds of cattle are allowed to graze in a particular pasture at a higher stocking density but for a shorter period, followed by longer periods of rest and recovery (Danvir et al. 2005). About 30% of DLL's pastures receive a full year's rest (Dahlgren et al. 2015a).

The 3C is a 56,900 ha consortium of 29 individual BLM and USFS grazing allotments and private lands that are generally managed under a combination of deferred rotational and season-long grazing, located northwest of the town of Randolph UT

(Payne 2011). Because 3C cattle are not allocated to specific pastures in specific periods like they are in DLL, reliable data regarding cattle distributions across pastures through time were unavailable for 3C, which limited our inference on the effects of grazing on sage-grouse habitat selection.

Vegetation on the study area is dominated by Wyoming big sagebrush (A. *tridentata wyomingensis*), black sagebrush (*A. nova*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), and mixed grasses and forbs at lower elevations. These plant communities transitioned into aspen (*Populous tremuloides*), Gambel oak (*Quercus spp.),* mountain big sagebrush (*A. t. vaseyana*), and mixed conifers and maple (*Acer spp*.) at higher elevations. The average precipitation in the summer is about 34.2 cm coming in the form of rain and an average of 173 cm of snowfall in the winter. The temperature ranges from 30.2° C in July to -16.2° C in January (Western Regional Climate Center. 2022).

METHODS

Sage-grouse Capture and Radio-Marking

Because we were initially interested in comparing sage-grouse vital rates between the grazing treatments, we focused on female sage-grouse and their brood success because they drive population growth (Caudill et al. 2014). From 2012-2020, we captured, radio-marked, and monitored female sage-grouse resulting in 97 individual broods and 4,580 locations. All trapping was done at night in minimal light conditions using spot lights, dip nets and traveling around leks by use of all-terrain vehicles. The spot light is used to first detect female sage-grouse and then capture with the dip nets following procedures described by Connelly et al. (2003). All females were fitted with either a 22g very-high frequency (VHF) necklace collar or a 22g PTT rump-mounted global positioning systems (GPS) transmitter.

Before each bird was released, location of capture (using a handheld GPS unit), age (determined by feather condition-adult/ juvenile; Braun and Schroeder 2015), and weight were recorded, as well as any additional comments regarding behavior or health of the bird. Birds were released as quickly as possible after processing in the same area of capture, in attempts to reduce capture myopathy. Each grouse was also fitted with a numbered aluminum leg band for further identification (National Band Company, Newport, KY). Protocol for trapping and handling of sage-grouse were obtained and approved by the Utah State University Institutional Animal Use and Care Committee permit #10111, and a UDWR Certificate of Registration #2BAND8744.

Radio-Telemetry

Although VHF collars are well suited to monitor sage-grouse vital rates, they do not provide adequate location data in terms of fix interval, or location accuracy. These data can best be obtained by GPS collars. GPS collars provide multiple locations per day, with a mean error radius of 3 meters, making them far better suited for evaluating our research objectives. The GPS transmitters also reduce problems with on-the-ground access, and eliminate observer disturbance of the bird. They also can provide real time data on survival, movements, habitat use, and timing of nest initiation. Recent technological advances have led to commercial production of smaller (22-30 g), solar powered, GPS satellite transmitters that can be mounted using a leg-loop harness (i.e., rump mounted) rather than backpack harnesses which biased survival estimates (Caudill et al. 2014).

The GPS transmitters were introduced to the study design in 2014. Radio-marked sage-grouse were located using radio telemetry to determine habitat-use patterns, seasonal movements, nesting and brood success, and survival rates. All spatial data were recorded in Universal Transverse Mercator (UTM), Zone 12, WGS 84.

Brood Monitoring

Sage-grouse typically lay 6-9 eggs, with surviving chicks called a “brood”. After a VHF-marked female was confirmed to have a successful nest, broods were located 1-2 times per week. A GPS coordinate was recorded for every brood location. Successfully hatched GPS-marked females were located once per week to determine brood fate. All broods were located using radio telemetry, the observer circled the suspected area reducing the radius with each lap until the marked grouse was visually located. The area was then carefully examined to determine presence or absence of chicks.

Monitoring of broods continued for 50 days post hatch, if females retain chicks at this time, broods were determined successful. If at any time within the 50-day period a female was flushed 2 consecutive times with at least one other adult sage-grouse and no chicks were seen, the brood was classified as unsuccessful and monitoring was reduced to once per week.

Data Analysis

Grazing data for DLL were obtained from the ranch managerial records spanning 2012-2020. From these records we obtained pasture names, date cattle were turned into each pasture, and date cattle were removed from each pasture by year. Because the grazing regime in 3C is a combination of deferred rotational and season-long rather than deferred-rest rotation, spatially-explicit information on grazing schedules was not available in this area, which limited our inference.

We used sage-grouse brood locations (2012-2020) to assess 3rd-order habitat selection of female sage-grouse on DLL and 3C. The 3rd-order habitat selection quantifies patterns of resource selection within an individual's home range (Johnson 1980). We fit Resource Selection Functions (RSF; Boyce et al. 2002, Manly et al. 2002) to quantify sage-grouse habitat selection in relation to vegetation dynamics and, where possible (DLL), livestock grazing. An RSF is based on a used vs. availability study design, where used points are compared to a set of random points capturing available conditions at the appropriate scale depending on the focal order of selection. Used points were gathered from sage-grouse GPS locations. To sample available conditions at the 3rd order, we constructed brood rearing home ranges for each individual using a Kernel Utilization Distribution (KUD; Worton 1989) approach. Guidelines for habitat selection modeling include using a number of available points that is as much larger as possible than the number of used points (Fieberg et al. 2021). Thus, we selected the 90% isopleth of the KUD (Börger et al. 2006) and sampled systematically within each home range every 30 m. Covariates that might help explain sage-grouse habitat selection included topography, vegetation cover, and vegetation dynamics (climate, water sources). We intersected used and available points with elevation and aspect (data from Landfire 2016), percent sagebrush cover (data from National Land Cover Database 2016), Normalized Difference Vegetation Index (NDVI; data from MODIS 2012-2020), and Instantaneous Rate of Greenup (IRG; computed from NDVI values). NDVI is an index of vegetation greenness, which can be correlated with biomass, while IRG is an index of vegetation growth (if positive) or senescence (if negative) (Tucker 1979, Bischof et al. 2012, Stoner et al. 2016). Because values of NDVI and IRG vary at the daily scale, we associated used points on each individual-day with the full set of available points within an individual's home range intersected with covariates on that day. For points within DLL, we also calculated the time since a location was last grazed. For 3C, data on grazing schedules was not available, thus we omitted the "time since last grazing" covariate for the model in this study area and only analyzed habitat selection as a function of topography and vegetation dynamics.

We fit the RSF using a conditional logistic regression model where used and available locations were stratified based on the combination of individual ID and date. We fit separate models to data from DLL and 3C. Because we expected the response to elevation, sagebrush, NDVI, and days since last grazed (where applicable) to potentially follow a unimodal trend, we fit quadratic terms to these predictors. We applied a sinusoidal transformation to aspect by including both the sine and cosine of aspect as predictors in the model. We also fit two-way interactions between NDVI, IRG, and (where applicable) days since last grazed. We quantified results in terms of log-Relative Selection Strength (log-RSS; Avgar et al. 2017) by dividing predicted probabilities of use across the range of each predictor by the probability of use of a hypothetical pixel where all predictors are fixed at their mean seasonal value, while holding all other predictors constant. The resulting metric expresses preference (if > 1) or avoidance (if < 1) of a predictor value versus the average conditions observed across the landscape.

RESULTS

Our final dataset included 31 individuals (14 in DLL and 17 in 3C) and 821 individual-days. Our dataset contained 9,027,543 points, of which 2,841 were used and 9,024,702 were available. Sage-grouse in summer selected for higher than average elevations in both DLL and 3C, and exhibited no selection for aspect in DLL or weak selection for northeast-facing slopes in 3C (Fig. 2). Sage-grouse exhibited no selection for sagebrush in DLL and weak selection for greater than average sagebrush percent cover in 3C (Fig. 2). Sage-grouse selected for intermediate values of NDVI in DLL and for higher than average values of NDVI in 3C (Fig. 2). Sage-grouse selected for lower than average IRG in DLL and did not exhibit selection for IRG in 3C when all other predictors were held at their mean value (Fig. 2). However, the response to IRG differed depending on the value of NDVI: at low NDVI values, sage-grouse in 3C selected for higher IRG, while they selected for lower IRG at high NDVI values; in DLL, sage-grouse selected for lower IRG regardless of NDVI. On DLL, sage-grouse avoided areas that were more recently grazed, i.e. under a year. (Fig. 2). This pattern of selection became stronger with increasing NDVI and it was not affected by IRG (Fig. 3).

DISCUSSION

Our results indicated that sage-grouse brood habitat selection at the 3rd order differed between DLL and 3C. In DLL, where grazing is managed using a deferred-rest rotation regime, sage-grouse selected for intermediate vegetation biomass and faster vegetation senescence; however, sage-grouse avoided areas that had been grazed within the past year. In 3C, where grazing is managed following a combination of deferred rotation and season-long grazing, sage-grouse selected for high vegetation biomass and did not respond to different rates of vegetation senescence. We were unable to test responses of sage-grouse to recent grazing in 3C. These results match our predictions in terms of selection for areas with optimal forage quality (which should correspond to intermediate biomass) in DLL but not in 3C; however, the avoidance of areas that were recently grazed in DLL did not match our predictions, suggesting that livestock grazing did not directly create the foraging conditions that sage-grouse selected for.

Under the hypothesis that livestock grazing affects vegetation dynamics by reducing biomass and thus making room for new plant growth (similar to bison; Geremia et al. 2019), we expected sage-grouse in DLL to select for pastures that had been grazed more recently that same season. Instead, sage-grouse in DLL coupled selection for intermediate biomass and fast senescence with avoidance of recently grazed pastures, which suggests the vegetation conditions sage-grouse are selecting for are not directly created by livestock grazing. However, it is possible that livestock grazing has carry-over effects on vegetation dynamics in the following season. For instance, in rested pastures, livestock grazing in the previous year may contribute to creating areas of intermediate biomass that sage-grouse select for in the following season. The deferred-rest rotation grazing system employed in DLL may allow for spatio-temporal segregation of cattle and sage-grouse, such that sage-grouse are able to avoid overlapping with livestock and may adjust their selection for vegetation to make the most of what remains available in pastures that are currently rested.

Selection for intermediate biomass is a common pattern observed across taxa for which green-wave surfing has been documented (van der Graaf et al. 2006, Merkle et al. 2016, Aikens et al. 2017). Intermediate biomass values often correspond to the highest nutritional value and thus the highest quality forage. In this sense, our findings matched our predictions for DLL. Because our analysis was restricted to the brood-rearing season, all values of IRG were negative, indicating senescence rather than green-up (e.g., a positive IRG value means NDVI is increasing through time during the spring green-up; a negative IRG value means NDVI is decreasing through time during the fall senescence).

Our results digress from the published literature on spring green-wave surfing so that expectations on the response to green-up rate may not translate directly. In other words, sage-grouse chicks hatch at or just before the peak of season (Stoner et al. 2020), and therefore most of the brood rearing period takes place when vegetation has peaked and is in decline. Nonetheless, the selection for faster senescence exhibited by sage-grouse in DLL seems suboptimal. There are three possible explanations for this phenomenon.

First, sage-grouse may be relegated to suboptimal habitat in DLL if they are avoiding pastures where cattle are present. Alternatively, sage-grouse may be selecting for areas that are senescing faster to exploit resources that are about to disappear, while areas with slower senescence are likely to be available for longer. Third, faster senescence could be indicative of forb-dominated areas, whereas slower senescence values could be associated with shrub-dominated areas, as forbs senesce faster than shrubs in the summer. In this case, selection for faster senescence by sage-grouse could simply indicate selection for forb-dominated areas.

In 3C where grazing is implemented following a combination of deferred rotation and season-long regimes, sage-grouse selected for high vegetation biomass and, when vegetation cover is high, for faster senescence (similar to DLL). Rather than selecting for intermediate vegetation biomass, which presumably corresponds to optimal palatability, sage-grouse select for high biomass, possibly prioritizing concealment over nutrition. Because 3C does not follow a prescribed grazing scheme, we were not able to test whether sage-grouse avoid being in the same areas at the same time as cattle as we observed in DLL.

Habitat treatments implemented on DLL previously may have also provided benefits to sage-grouse, weather in conjunction with prescribed grazing or independently. Sagebrush treatments on DLL were various in size but generally < 200-ha carried out in mosaic patterns. Treatments were generally done in sagebrush communities above 2000m elevation (Connelly et al. 2000, Dahlgren et al. 2015a). These treatments were shown to have increased herbaceous cover and production (Aoude 2002, Summers 2005). Dahlgren (2015a) suggested the treatments could have increased the availability of grasses and forbs (Slater 2003, Dahlgren et al. 2006a, Stringham 2010), allowing more resources for sage-grouse. Dahlgren (2015a) also suggested that the productivity of the sagebrush treatments was allowed to persist because of the deferred-rest rotation grazing employed on DLL allowing pasture to rest during the growing season (Davies et al. 2011). When used together sagebrush treatments and prescriptive grazing can promote plant heterogeneity which has been shown to be beneficial to sage-grouse (Boyd et al. 2011).

This research adds new information to the literature pertaining to the knowledge gap between livestock grazing and whether it is facilitative or competitive with brooding sage-grouse. Our results suggest that the relationship between livestock and sage-grouse might be competitive on the short term but facilitative over longer time scales. These findings indicate that deferred-rest rotational grazing practices may allow for spatio-temporal segregation, enhancing the capacity for sage-grouse to optimize the exploitation of available forage while avoiding direct contact with livestock. Because of the DLL grazing strategy sage-grouse on that site have the ability to avoid cattle while potentially benefitting from the legacy effects of deferred-rest rotation grazing practices. However, the lack of data on livestock distribution in 3C meant we were not able to compare sage-grouse behavior in relation to livestock presence in the two study areas. Further research could focus on directly comparing sage-grouse responses to livestock distribution in various types of grazing management systems, determining whether different systems may aggravate or alleviate any competitive mechanisms between sage-grouse and livestock. Further, our results suggest that livestock grazing could have carry-over effects on vegetation dynamics that may benefit sage-grouse in subsequent seasons, although we did not test this directly; more research is needed to understand the effects of livestock grazing across multiple growing seasons.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Over 50% of the earths terrestrial landscapes are considered rangelands (Sala et al. 2017). Briske et al. (2017) defined rangelands as uncultivated lands dominated by grasses, forbs, and shrubs that are suitable for grazing by livestock, habitat for wildlife, and provide humans with ecosystems services. However, improper grazing (over stocking or over grazing) by livestock has been implicated as a threat to wildlife conservation (Krausman et al. 2009, Robinson et al. 2019). The prairie grouse species that inhabit rangelands of North America are considered some of the most imperiled and at the greatest risk to improper livestock grazing practices (Silvy and Hagen 2004). With a projected increase in demand for livestock products (Thornton 2010), better information will be required to understand the effect grazing may have on sage-grouse.

Here, we analyzed brood habitat selection of sage-grouse in response to vegetation dynamics and, where possible (DLL), included an interaction with livestock grazing to determine whether the relationship between sage-grouse and cattle is competitive or facilitative. First, we hypothesized that sage-grouse would select for high-quality forage by selecting for intermediate values of biomass (e.g., usually associated with high palatability; Hebblewhite et al. 2008) both in DLL and 3C. Second, in DLL, we tested the hypothesis of a facilitative relationship between livestock and sage-grouse, according to which prescriptive grazing could promote rejuvenation of forage resources that support the needs of sage-grouse through the brood rearing period; under this hypothesis, we predicted that sage-grouse would select for recently grazed areas. Conversely, if the relationship between livestock and sage-grouse is competitive, we predicted sage-grouse would avoid recently grazed areas.

This research adds new information to the literature pertaining to the knowledge gap between livestock grazing and whether it is facilitative or competitive with brooding sage-grouse. Our results suggest that the relationship between livestock and sage-grouse might be competitive on the short term but facilitative over longer time scales. These findings indicate that deferred-rest rotational grazing practices may allow for spatio-temporal segregation, enhancing the capacity for sage-grouse to optimize the exploitation of available forage while avoiding direct contact with livestock. Further, our results suggest that livestock grazing could have carry-over effects on vegetation dynamics that may benefit sage-grouse in subsequent seasons, although we did not test this directly; more research is needed to understand the effects of livestock grazing across multiple growing seasons.

Because livestock grazing is the predominant land-use on western rangelands inhabited by sage-grouse, understanding how to balance competitive and facilitative effects of livestock grazing on sage-grouse populations is critical to effectively manage rangelands for both. To provide conclusive evidence of which management systems enhance facilitation while attenuating competition, managers and researchers should engage in a concerted effort to experimentally test the effects of different grazing regimes on sage-grouse populations. Recording detailed information on the spatio-temporal distribution of cattle across pastures is especially critical.

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FIGURES

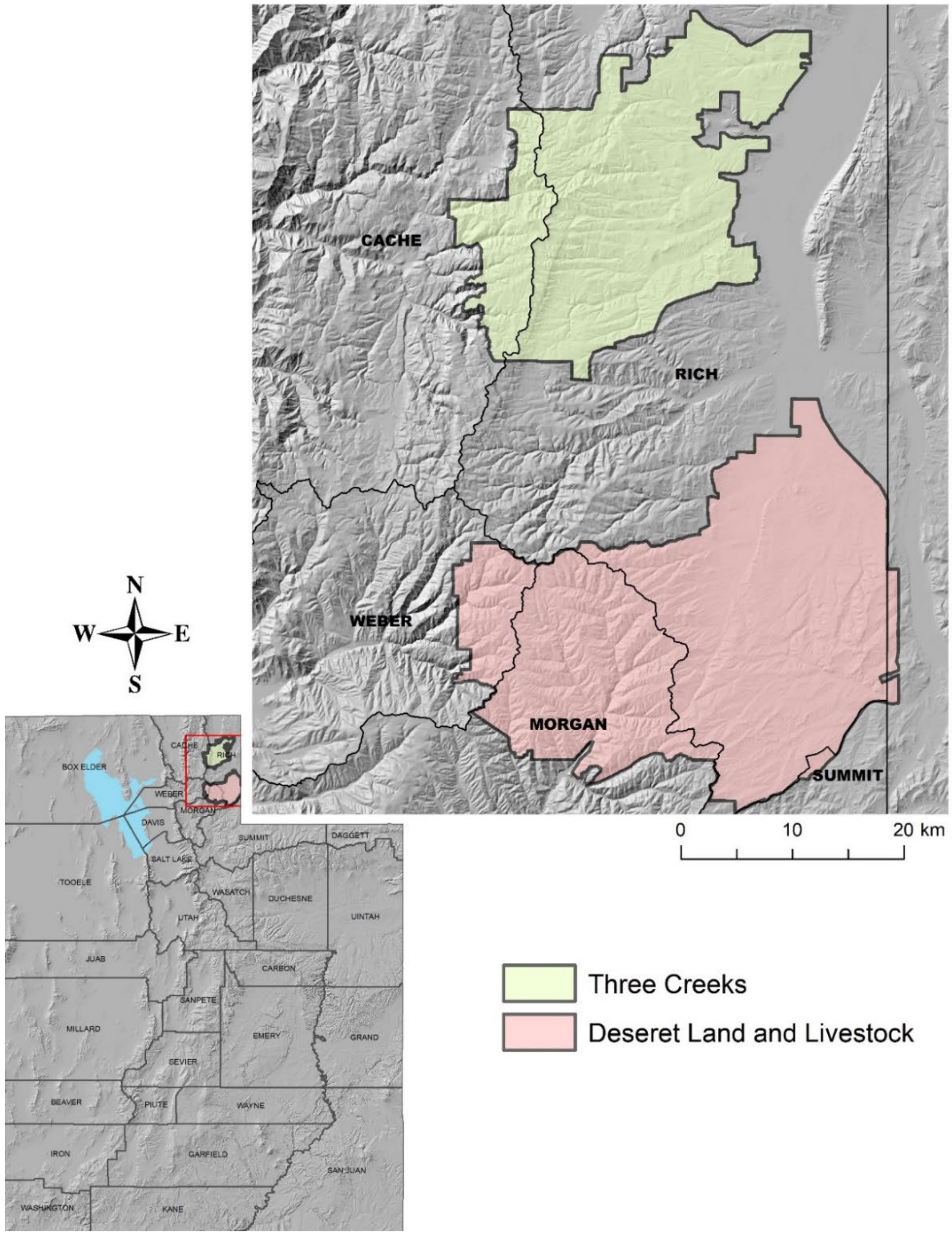

Figure 1 -- Northeastern Rich County, Utah, United States study area for greater sage-grouse *(Centrocercus urophasianus)* within the Rich-Morgan-Summit Sage-grouse Management Area. It consisted of the Deseret Land and Livestock (DLL), an 86,900 ha privately owned ranch, and Three Creeks (3C), a 56,900 ha consolidation of private land, Bureau of Land Management and U.S. Forest Service grazing allotments, 2012-2020.

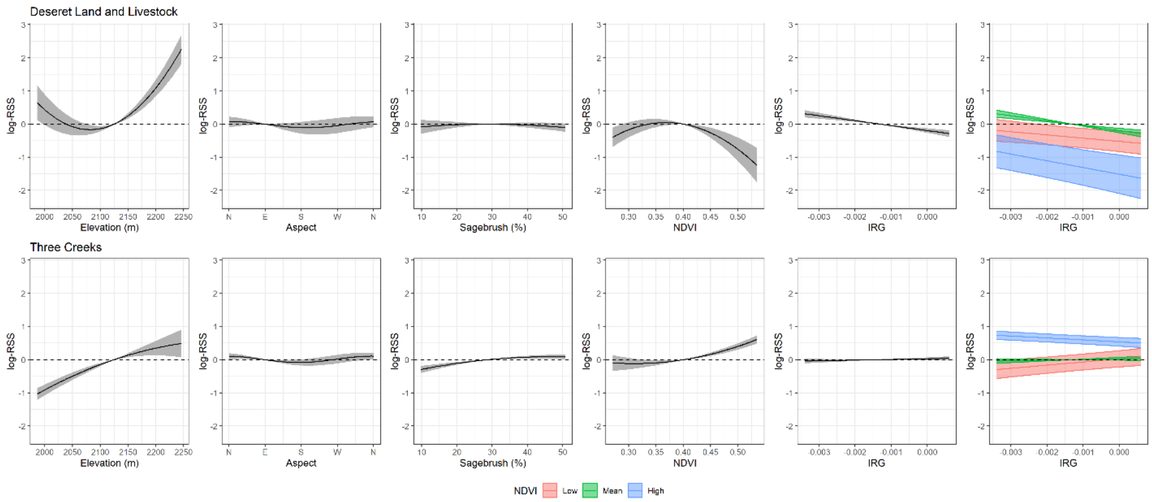

Figure 2 – Resource Selection Function (RSS) results quantifying the response of female greater sage-grouse (*Centrocercus urophasianus*) radio-marked and monitored from 2012-2020, to topography and vegetation variables on Deseret Land and Livestock (DLL, top) and the Three Creek Grazing Allotment (3C, bottom). The curve indicates Relative Selection Strength (RSS) for different values of each predictor, all other predictors being held at their mean value. Log-RSS values above 0 indicate selection with respect to the average value, whereas values below 0 indicate avoidance. The shaded ribbon depicts 95% confidence intervals.

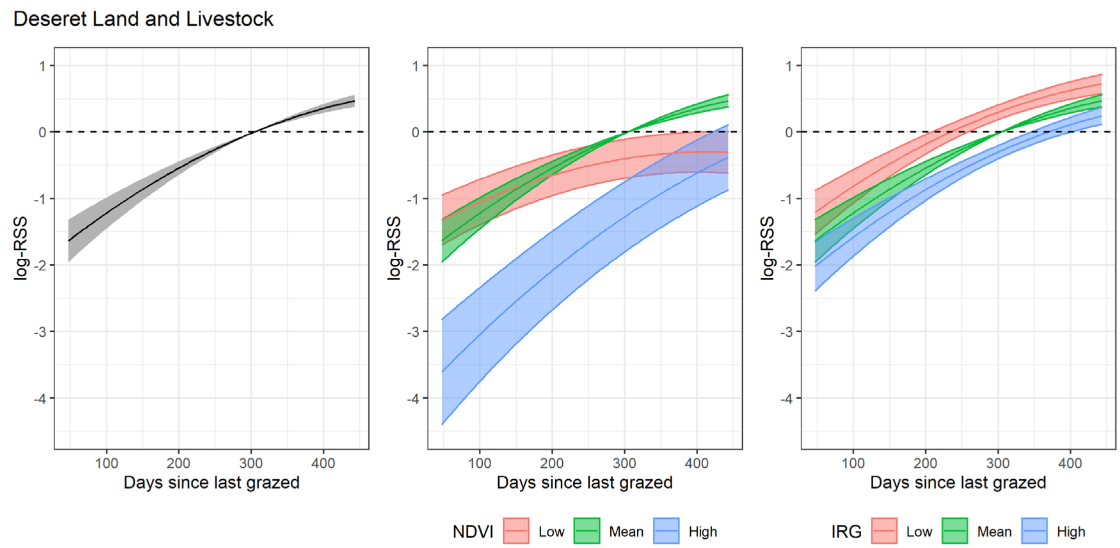

Figure 3 – Results of Resource Selection Function (RSS) quantifying the response of female greater sage-grouse (*Centrocercus urophasianus*) radio-marked and monitored from 2012-2020, to the time since the last grazing event on Deseret Land and Livestock (DLL). The curve indicates Relative Selection Strength for different values of days since grazed, all other predictors being held at their mean value. Log-RSS values above 0 indicate selection with respect to the average value, whereas values below 0 indicate avoidance. The shaded ribbon depicts 95% confidence intervals.