Patterns of nest survival, movement and habitat use of sagebrush-obligate birds in an energy development landscape

by

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Examining Committee Membership

The following served on the Examining Committee for this thesis. The decision of the Examining Committee is by majority vote.

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AUTHOR'S DECLARATION

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners. I understand that my thesis may be made electronically available to the public.

Statement of Contributions

Christopher Paul Kirol was the sole author of Chapters 1 and 6, that were written under the supervision of Bradley Fedy and were not written for publication.

This thesis consists of four (4) manuscripts that have been published or prepared for publication. I was a lead author of three (3) of these manuscripts. As lead author, I contributed to developing the study design, applying for funding, applying for research permits, procuring field equipment, organizing field logistics, hiring seasonal technicians, supervising technicians, carrying out data collection and analysis, writing reports for funding and permitting agencies and drafting and submitting manuscripts. My supervisor and coauthors provided guidance and feedback during each step of the research process and manuscript drafting.

Exceptions to sole authorship of material are as follows:

Chapter 2 of this thesis was published in 2018 in the Wildlife Society Bulletin (citation below). Andrew L. Sutphin was the lead author of this manuscript. As a coauthor I contributed to carrying out data collection and analysis and drafting and submitting the manuscript.

Sutphin, A. L., T. L. Maechtle, C. P. Kirol, and B. C. Fedy. 2018. A mobile tool for capturing greater sage-grouse. Wildlife Society Bulletin 42:504–509.

Chapter 3 of this thesis was published in 2020 in the Wildlife Society Bulletin (citation below). I was responsible for all aspects of manuscript preparation outlined above and received input and feedback from my coauthors Bradley Fedy, Dylan Kesler and Brett Walker.

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Chapter 4 of this thesis has been submitted to an avian ecology journal. I was responsible for all aspects of manuscript preparation outlined above and received input and feedback from my coauthor Bradley Fedy.

Chapter 5 of this thesis is being prepared for submission. I was responsible for all aspects of manuscript preparation outlined above and received input and feedback from my coauthor Bradley Fedy.

In addition to the chapters included in this thesis, I coauthored two (2) manuscripts. Both of these manuscripts were led by Natasha Barlow. As a coauthor I contributed to many of the aspect of the preparation of these manuscripts outlined above. The first manuscript was published in the Journal of Wildlife Management in 2019 and the second was in Biological Conservation in 2020 (citations below).

Barlow, N. L., C. P. Kirol, K. E. Doherty, and B. C. Fedy. 2019. Evaluation of the umbrella species concept at fine spatial scales. The Journal of Wildlife Management 84:237–248.

Barlow, N. L., C. P. Kirol, and B. C. Fedy. 2020. Avian community response to landscape-scale habitat reclamation. Biological Conservation 252:108850.

Throughout this thesis I use the pronoun ‘we’ in place of ‘I’ to reflect the collaborative nature of this work. Specifically, the collective ‘we’ refers to my collaborators and coauthors of each independent manuscript. I follow the Journal of Wildlife Management style guidelines throughout the thesis.

Abstract

The sagebrush ecosystem in western North America provides habitat for approximately 350 plant and animal species, many of which are species of conservation concern. The sage-grouse and several species of sagebrush associated songbirds have undergone population declines over the last fifty years. Energy development has been identified as one of the leading causes of sagebrush landcover loss and fragmentation and has contributed to declines of sagebrush dependent bird species. Our research represented management-oriented science related to the conservation of sagebrush associated species. We used a sagebrush-obligate songbird, the Brewer's sparrow (*Spizella breweri breweri*), and the greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) to address questions related to habitat selection, space use, reproductive rates and movements in an established energy field in the Powder River Basin (PRB) in Wyoming, USA.

Attaching global positioning system (GPS) tags to wildlife can provide a tremendous amount of information that can be used to better understand many aspects of a species' ecology and how wildlife may be responding to anthropogenic disturbances. Information gathered from tracking wildlife is critical to inform management and conservation actions designed to benefit species that are being effected by anthropogenic activities. To minimize impacts and increase capturing efficiency when capturing sage-grouse to attach GPS tags, we developed a new mobile capturing technique. We had a 71% capture success rate. The capturing method we describe proved effective in our study and we believe this method can be applied to other bird species with similar behavioral traits.

For most wildlife species, researchers must select between multiple tracking technologies that represent trade-offs among data requirements, mass, and cost. Options tend to be more limited for smaller species and those that fly. To address our research question, we developed and tested a unique combination of a store-on-board GPS logger with an independent very-high-frequency (VHF) tag (hereafter hybrid tag) fitted on sage-grouse with a modified harness design. We compared the hybrid tag we designed with other tracking technologies commonly used in bird research, namely VHF and Argos satellite relay tags. Given our research objectives, that required both frequent location data and field-based observational data, we found hybrid tags were the most cost-effective option and capable of collecting more location data compared with Argos tags because of power savings associated with data transmission. Cost savings allowed us to avoid sacrificing sample size while still obtaining high-resolution location data in addition to field-based observational data such as the presence of sage-grouse chicks. We believe our hybrid tags and harness design would be beneficial to research on other bird species of comparable size to sage-grouse and those that are relatively localized year-round, including many other Galliformes.

Habitat selection in wildlife occurs across multiples spatial scales from selection for broad geographic areas to fine-scale habitat components. Therefore, the selection scale of interest in a study must dictate the spatial extent of the area considered as available to the species and availability should be based on biologically realistic movements of that species or individual. Habitat selection studies are usually conducted at a population level. Habitat selection analyses at an individual level can reveal patterns in selection that are not apparent when using population-level approaches. The hybrid tag, that allowed for gathering high-resolution location and movement data, and new data analyses approaches allowed us to explore individual-level movements, space use (e.g., home ranges) and habitat selection of female sage-grouse that raised chicks (brood-rearing sage-grouse) in a coal-bed natural gas (CBNG) development area. We used integrated step selection analysis (iSSA) that permit the quantification of the effects of environmental and anthropogenic covariates on the movement and selection process simultaneously to evaluate habitat selection and avoidance behaviors. On average, brood-rearing female sage-grouse established home ranges in areas with a majority of the home range comprised of sagebrush landcover (mean = 77.4%) and a minimal proportion of the area comprised of anthropogenic surface disturbance (mean = 3.5%). Individual-level selection analyses helped us uncouple some aspects of energy development that influence habitat selection that likely would not have been detected at broader spatial scales. Brood-rearing females consistently selected for natural vegetation and avoided disturbed surfaces, including reclamation surfaces, at fine spatial scales. Power line visibility generally led to avoidance behavior; however, much shorter (3m) CBNG well structures generally did not. We found that individual variability was partially explained by age (adult or first year), or previous experience of the landscape. Our results do not support individual uniformity in brood-rearing sage-grouse and reiterate the importance of accounting for, or at least recognizing, individual variability in population-level modeling efforts.

Reclamation is increasingly emphasized as a means of mitigating impacts on species that have been affected by oil and gas development; however, the response of sagebrush species to reclamation has largely been untested. We used the Brewer’s sparrow nest survival as an indicator of population fitness responses to early-stage reclamation in sagebrush habitat. Addressing the question: does early-stage reclamation of energy disturbance provide a population benefit for the Brewer’s sparrow? We assessed oil and gas reclamation approximately five years after reclamation, but sagebrush reestablishment is a slow process; thus, the legacy of these disturbances (i.e., disturbance scars) will likely remain for decades. We compared Brewer’s sparrow nest survival across a gradient of oil and gas development from undisturbed and active development to areas that have undergone oil and gas reclamation. Nest survival was assessed at multiple scales from microhabitat to landscape. Our study was designed to also help us better understand the mechanisms that act to depress songbird nest survival in oil and gas development fields (i.e., physical footprint of disturbance or infrastructure features). The distribution of nest sites in the active CBNG development and reclamation treatments suggested local avoidance of disturbance, both active disturbance and reclamation, when establishing nesting territories. We found that reclamation benefited nest survival at a local scale which suggests that infrastructure, and associated human activity, may be more influential on Brewer’s sparrow nest predation risk than the physical footprint of disturbance alone. Our findings demonstrated scale-dependent nest survival relationships. Across microhabitat and landscape scales, sagebrush canopy cover and composition are important to Brewer’s sparrow reproductive success. Combined, these findings emphasize the importance of avoiding the removal of sagebrush habitat whenever possible and expediting sagebrush regeneration in disturbed areas to maintain suitable sagebrush habitat for breeding songbird populations.

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Chapter 1

Introduction

1.1 Sagebrush ecosystem

Sagebrush (*Artemesia* spp.) vegetation communities occurs in cold semi-deserts across the intermountain west and these vegetation communities form the largest shrub ecosystem in North America (Anderson and Inouye 2001, Knick et al. 2003). However, anthropogenic disturbance including conversion to agriculture, urban expansion and industrial development have reduced the sagebrush ecosystem extent by ~50% (Connelly et al. 2004, Schroeder et al. 2004). Much of the remaining sagebrush ecosystem is extensively fragmented by anthropogenic disturbances and degraded by the invasion of non-native plant species (Knick et al. 2011 and Leu and Hanser 2011). Recent estimates suggest that in North America, the area disturbed by oil and gas development built from 2000 to 2012 is equivalent to the land area of three Yellowstone National Parks (~3 million ha; Allred et al. 2015) and much of this energy disturbance overlaps the sagebrush ecosystem. For instance, the Powder River Basin (PRB) in northeastern Wyoming, USA is within the sagebrush ecosystem and energy development that occurred in this area in the early 2000s involved the drilling of more than 27,522 natural gas wells and associated supporting infrastructure including an estimated 9,656 km of overhead power lines (Knick et al. 2011). The state of Wyoming contains about 21% of remaining sagebrush landcover in North America and; therefore, is critical to the long-term conservation of the sagebrush ecosystem (Connelly et al. 2004). Wyoming is also one of the largest producers of domestic energy in the United States and much of the current and forecasted energy development, both renewable and nonrenewable, overlaps the sagebrush ecosystem in the state (Knick et al. 2011, Copeland et al. 2013, Kirol et al. 2020a).

This sagebrush ecosystem provides habitat for approximately 350 plant and animal species, many of which are species of conservation concern (Davies et al. 2011, Rowland et al. 2011). The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) has become a flagship species representing the plight of the sagebrush ecosystem in the face of an expanding anthropogenic footprint (Hebblewhite 2017). The sage-grouse and several species of sagebrush associated songbirds have undergone population declines over the last 50 years (Knick et al. 2003, Garton et al. 2011, Rosenberg et al. 2016). Sagebrush associated songbirds that have declined and are species of conservation concern include Brewer's sparrow (*Spizella breweri breweri*) and the sage thrasher (*Oreoscoptes montanus*; Rosenberg et al. 2016).

Energy development has been identified as one of the leading causes of sagebrush landcover loss and fragmentation and has contributed to declines in co-occurring bird populations (USFWS 2010, Knick et al. 2011). Energy development can directly affect bird populations through direct mortality and reduced reproductive rates (e.g., nest success; Bayne and Dale 2011, Naugle et al. 2011, Bernath-Plaisted and Koper 2016, Kirol et al. 2020*a*). The physical footprint of energy development results in the direct loss of sagebrush habitat and the fragmentation of sagebrush landcover into smaller patches. However, the ecological footprint of energy development is often much larger than the physical footprint because energy infrastructure, industrial noise and human activity (e.g., vehicle traffic) cause birds to avoid otherwise suitable habitats at local and landscape scales (sensu Naugle et al. 2011, Bayne and Dale 2011, Blickley et al. 2012). The indirect loss of habitat due to avoidance behaviour is often referred to as functional habitat loss.

Studies designed to uncouple the diverse impacts of energy development on co-occurring species are critical to inform effective mitigation strategies and conservation planning. A more mechanistic understanding of energy impacts on wildlife will help us more effectively mitigate these impacts (Northrup and Wittemyer 2012). A lot has been learned about impacts of energy development on co-occurring sagebrush birds through studies on presence/absence, species richness and population trends (e.g., Walker et al. 2007, Gilbert and Chalfoun 2011, Barlow et al. 2020). However, studies assessing behavioral and reproductive responses to energy development, like habitat selection, avoidance behavior, movement, space use, and reproductive outcomes, help us better understand the mechanisms and specific components of energy development that drive negative trends in sagebrush bird populations (e.g., Doherty et al. 2008, Bernath-Plaisted and Koper 2016).

Energy development in the form of oil and gas typically includes clearing natural vegetation for well pads and compressor sites, a network of roads to connect infrastructure, pipeline corridors to transport the fluid minerals and, in some cases, wastewater reservoirs (Walker et al. 2007, Allred et al. 2015). Studies have shown that sage-grouse nest success is consistently lower in oil and gas development areas when compared to non-developed areas (Connelly et al. 2011*a*). Previous research on the effects of coal-bed natural gas (CBNG) found little evidence for relationships between nest success and the proximity to roads and CBNG wells or road and well densities as hypothesized, but found that the presence of CBNG reservoirs was driving reduced nest success of sage-grouse in development areas (Kirol et al. 2015*b*). While acknowledging that a combination of multiple energy-related factors led to negative responses in birds and some of these impacts may be synergistic (Naugle et al. 2011, Bayne and Dale 2011), it is important to understand if certain components of energy development are particularly detrimental to co-occurring bird species. With this information management can target the most detrimental energy components to increase the effectiveness of mitigation and conservation actions (Northrup and Wittemyer 2012). In addition, knowledge of impacts of specific energy development components can often be transferable between energy development types, both renewable and nonrenewable, because different energy development types share many characteristics and infrastructure components (Naugle et al. 2011). For instance, oil and gas and wind energy both require a network of roads to access sites and power lines to transport electricity. Unlike other energy sources, oil and gas development is generally considered a temporary disturbance because of the finite capacity of oil and gas production within areas and post-development reclamation that is usually mandated under conditions of approval (Andersen et al. 2009, Clement et al. 2014).

1.2 Sagebrush reclamation

Because of the continued loss and fragmentation of sagebrush landcover, state and federal agencies are putting greater emphasis on reclamation of disturbed sites and restoration of sagebrush vegetation communities as a mitigation strategy to reduce impacts of energy development and moderate the net loss of sagebrush habitat (BLM 2004, USFWS 2010, Clement et al. 2014, State of Wyoming 2019). Yet, there is a lack of information to determine if site reclamation and habitat restoration can effectively mitigate impacts of development on wildlife, especially in sagebrush habitat (Bayne and Dale 2011, Pyke 2011, Pyke et al. 2015). The idea that wildlife species will respond immediately to habitat restoration has been described as the “if you build it, they will come” assumption (Perring et al. 2015). But the response of wildlife to site reclamation and habitat restoration is often slow (Schaid et al. 1983, Evangelista et al. 2011), and highly specialized species, such as the greater sage-grouse, may be even slower to respond. Reclamation generally refers to the rebuilding of soil profiles to reestablish plant communities (Pyke et al. 2015). In areas disturbed by energy development, reclamation is the first step in habitat restoration efforts (BLM 2004, Pyke et al. 2015, State of Wyoming 2019). In the context of sagebrush habitat management, habitat restoration refers to the process of recovering sagebrush vegetation communities that has been degraded, damage, or destroyed with a goal of achieving pre-disturbance structure and function (BLM 2004, USFWS 2010, State of Wyoming 2019). Reestablishment of sagebrush and the associated vegetation communities is challenging because succession proceeds slowly in these arid systems (Baker 2011). For instance, big sagebrush (*Artemisia tridentata*), the dominate shrub species in sagebrush ecosystems, can take from 25 to 125 years to return to pre-disturbance size and structure through natural reestablishment (Baker 2011, Avirmed et al. 2015). Consequently, the legacy of energy disturbance ─ disturbance scars that fragment and reduce patch size of sagebrush landcover ─ will also persist for decades in these areas unless active restoration (e.g., sagebrush planting) is applied to the reclaimed surfaces (Pyke et al. 2015).

Restoration of sagebrush vegetation communities after disturbance is often complicated by invasive plants that can become established on and adjacent to energy development areas and may slow or prevent the reestablishment of sagebrush plants (Evangelista et al. 2011, Miller et al. 2011). Invasion by the invasive cheatgrass (*Bromus tectorum*), for example, can increase the frequency and intensity of fires which can lead to potentially irreversible loss of sagebrush landcover (Miller et al. 2011, Reisner et al. 2013, Coates et al. 2016).

1.3 Wildlife tracking and capture

Marking and tracking of wildlife using telemetry is an important tool in wildlife research and data gathered from telemetry studies have substantially expanded our understanding of impacts of anthropogenic development on wildlife. For smaller and lighter volant species, telemetry options are more limited because of restrictions in the mass and size of the transmitter relative to the mass and size of the study species (Barron et al. 2010, Fair et al. 2010). However, technology advances are allowing for the production of smaller and lighter transmitters (hereafter tags; Bridge et al. 2011). The most appropriate tracking technology for a study depends on the study objectives, which dictate study needs such as required sample size, frequency of location data, and precision of locations. For most studies, costs of the different transmitter technologies are often a deciding factor because of budget limitations. Researchers often end up sacrificing sample size (number of tagged individuals) to allow for the purchase of tags that gather frequent and precise GPS location data because of the high costs associated with these tracking technologies. The higher cost satellite-based tracking technologies do not require any tracking or monitoring in the field and the location data is sent to your computer. Hebblewhite and Haydon (2010) argue that emerging GPS-tracking technologies should not replace field biology but be used in a way that augments data gathered through field work, allowing for a more complete understanding of animal behavior and ecology.

Sage-grouse are one of the most extensively researched species in North America. The first sage-grouse were fitted with radio transmitters in 1965 (Eng and Shladweiler 1972). Consequently, this species provides valuable information on implementation of new and old tracking technologies and attachment methods that are applicable to many less-studied avian species. The earliest radio transmitter or very-high-frequency (VHF) tags fitted on sage-grouse weighed 70 grams and had a battery life of less than a month (Connelly et al. 2003). The mass of VHF tags commonly used on sage-grouse today are 17 to 22 g (≥ 1.5% of the mass of an adult female) and have a battery lifespan of approximately 2 years (Walker et al. 2016). VHF tags generally require researchers to track the study species in the field to collect location data by using hand-held GPS units to mark the approximate location where they find the animal. Location data obtained from VHF tags are labor-intensive, infrequent, and prone to human error and may also be constrained by limits on access due to weather, road conditions, or land ownership (Withey et al. 2001, Hebblewhite and Haydon 2010). Sage-grouse studies using VHF tags generally only gather one or two GPS locations per week per individual (Walker et al. 2016, Kirol et al. 2020*a*).

More recently, solar powered Argos satellite relay tags (hereafter Argos tags) are being used in sage-grouse research (Smith et al. 2016, Pratt et al. 2017). The Argos tags fitted on sage-grouse can transmit >9–15 locations/day directly to the researcher's computer, via satellite relay, and; therefore, require no field work to obtain the location data (Smith et al. 2016, Pratt et al. 2017). Argos tags have an unlimited battery life expectancy because the batteries are charged by a solar panel positioned on the top of the unit. The initial purchase cost of Argos tags are approximately 20 times greater than VHF tags and costs of Argos systems increase with the download frequency because of additional satellite data download fees (Hebblewhite and Haydon 2010, Thomas et al. 2011).

To address my research questions, I needed to gather observational data in the field to know, for example, if a female sage-grouse had a successful nest attempt and if she raised her chicks to independence. My study objectives required gathering frequent location data while also having a suitable sample size of tagged sage-grouse and, like most studies, my study had a limited budget. None of the existing tags were ideal for my study needs. Therefore, I designed a tag that coupled two types of tracking technologies into one tag that had initial purchase costs that were 2.5 times less than Argos tags, allowing us to have a larger sample of tagged female sage-grouse. The 'hybrid' tag I designed was a combination of a store-on-board GPS logger with an independent VHF tag. Sage-grouse fitted with the hybrid tag were tracked in the field using traditional VHF tracking techniques. Once tagged sage-grouse were located, location data was downloaded from the GPS loggers using mobile UHF base stations and unidirectional antennas. Estimating the net cost per datum (e.g., GPS location) of different tracking technologies has been shown to be a valid way to compare costs of different tracking technologies (Thomas et al. 2011). Based upon the objectives of my study, I compared costs per datum of VHF tags, Argos tags, and hybrid tags. In addition, I described advantages and disadvantages of each type of tag in the context of research that require both field-based observational data and high-frequency and precise GPS location data.

Over the last five decades there have been several methods developed to capture sage-grouse for tagging. The most common methods used are rocket- or cannon-netting and spotlighting (Lacher and Lacher 1964; Wakkinen et al. 1992). Spotlighting has been widely used and proven effective for capture in many areas. This method of capture involves locating sage-grouse at night with a spotlight from truck, all-terrain vehicle, or on foot and capturing them with a hoop net. However, spotlighting is largely ineffective in areas with low sage-grouse population densities because of the difficulty in locating roosting sage-grouse at night is areas with few grouse. Rocket-netting involves deploying a large net (~37m long x ~12m wide) over a sage-grouse lekking site in the early morning when the lek is most active. Black powder charges detonate projectiles attached to the net, carrying the large net over the target. Compared to other methods, rocket-netting has a higher probability of resulting in injury or mortality of captured grouse (Silvy et al. 1990). Rocket-netting can also be dangerous to the capture crews and presents a fire hazard because of the use of black powder charges that must be stored and handled under strict safety protocols (Silvy et al. 1990).

Spotlighting was ineffective in my study area because of the low densities of sage-grouse. Furthermore, I elected not to use rocket-netting for many reasons including the increased likelihood of injuring sage-grouse during capture. I collaborated with others to develop a new method to capture sage-grouse that proved effective in my study area and alleviated some of the concerns I had with other capture methods including minimizing potential injuries in captured grouse, reducing set-up time and difficulty, and reducing disturbance of lekking activities. While modifying existing tracking technologies to design a tag that met my research needs and creating a new more cost-effective capturing technique, I hope to advance capturing and tracking technologies in bird research.

1.4 Study background

My study was in the PRB in northeastern Wyoming, USA. The PRB is on the eastern edge of the sagebrush ecosystem. The sage-grouse population in this region provides a critical genetic link to sage-grouse populations on the edge of the current sage-grouse range in North Dakota, South Dakota and eastern Montana, USA (Row et al. 2018). The PRB has a long history of energy development, primarily in the form of oil and gas and coal mining. Coal-bed natural gas (CBNG) development became widespread throughout the PRB between 2000 and 2015 and many previously undisturbed sagebrush habitats were developed for CBNG reserves during this timeframe (Walker et al. 2007, Doherty et al. 2008). While CBNG reserves were being developed (i.e., CBNG development phase) several research projects were conducted that explored impacts of the largescale CBNG development on sage-grouse and the effectiveness of on-site mitigation measures that were being used (Walker et al. 2007, Doherty et al. 2008, Fedy et al. 2015, Kirol et al. 2015*b*). Over this period of development, researchers documented substantial population declines in sage-grouse, which questions the long-term viability of sage-grouse in the PRB (Walker et al. 2007, Garton et al. 2011, Taylor et al. 2013).

It is common for studies of impacts of energy development to take place during the early stages of development (i.e., development phase) when the impacts are first occurring (Hebblewhite et al. 2011, Naugle et al. 2011). Studies on impacts of energy development on co-occurring wildlife that occur during the production phase of development, when the infrastructure is in place and construction has largely subsided, are much less common (Sawyer et al. 2009, Hebblewhite 2011, Kalyn Bogard and Davis 2014). Because of the reduction in traffic, heavy machinery (e.g., drilling rigs), industrial noise and human presence, the environment experienced by the animal is much different during the production phase than during the development phase (Ingelfinger and Anderson 2004, Sawyer et al. 2009). Therefore, studies conducted during the later stages of energy development (i.e., production phase) are needed to form a more holistic understanding of energy impacts on wildlife species (Hebblewhite 2011). The sage-grouse and Brewer’s sparrow used in my research represent multiple generations that have survived and reproduced in this industrial landscape. Therefore, the history of energy development and research in my study area provides for a unique opportunity to explore long-term effects of energy development on successive generations of sagebrush associated birds and build upon the early research conducted in this area.

1.5 Dissertation organization

The overarching goal of my dissertation research was to increase our collective understanding of the responses of sagebrush associate birds to established energy development and early-stage reclamation to inform management and conservation of birds impacted by energy development. In Chapter 2, I discuss a new method to capture sage-grouse. This method increased capturing efficiency in my study area, that contained a low density of sage-grouse, and minimized capturing impacts on sage-grouse when compared to other commonly used capturing methods. This work was published in the Wildlife Society Bulletin journal in 2018 (Sutphin et al. 2018). In Chapter 3, I discuss a unique transmitter I designed for this research that combined existing tracking technologies into one tag and a harness I designed to reduce negative effects of attaching rump-mounted tags on sage-grouse. I compared the tag I designed (hybrid tag) to other tracking technologies commonly used in prairie grouse research, namely VHF and Argos satellite relay tags. Through a cost assessment, I compared costs of each tracking technology. This work was published in the Wildlife Society Bulletin journal in 2020 (Kirol et al. 2020*b*). In Chapter 4, I use nest survival of the Brewer's sparrow to understand how this critical reproductive rate in birds is affected by early-stage reclamation of energy disturbance sites in sagebrush habitats. I compare nest survival across a gradient of oil and gas development from undisturbed and active development to development areas that have undergone site reclamation. I assess nest survival across multiple scales and explore both anthropogenic and environmental factors that affect nest survival in this sagebrush-obligate songbird. This work is in review at an avian ecology journal. In Chapter 5, I explore individual-level movements, space use (e.g., home ranges) and habitat selection of female greater sage-grouse that raised chicks (brood-rearing sage-grouse) in this energy development landscape. Using an analysis method that simultaneously incorporates the movement and selection processes, I explore effects of environmental and anthropogenic covariates on habitat selection and avoidance behaviors. I use these individual-based models to uncouple the impacts of different components of energy development on sage-grouse during the brood-rearing life stage. Finally, in Chapter 6, I discuss the management and conservation implications of my research findings and discuss future research needs.

Chapter 2

A mobile tool for capturing greater sage-grouse

2.1 Abstract

Capturing greater sage-grouse (*Centrocercus urophasianus*) using standard approaches can be challenging and inefficient, particularly in areas with relatively small populations and patchy habitat. In areas with low population densities, traditional trapping techniques such as drop netting and spotlighting have been largely ineffective. To increase trapping efficiency in such situations, we developed a new method to capture greater sage-grouse in Wyoming, USA, during spring and fall 2008-2011. We captured 92 sage-grouse (30 adult hens, 57 yearling hens, 3 hatch year hens, and 2 adult males) using a CODA net launcher modified to mount on a front receiver of a truck or all-terrain vehicle (ATV). We had 71% success (82 successful captures of one or more grouse in 115 attempts). We captured grouse during spring on the periphery of leks, to reduce disturbance of lekking behavior, and during fall along gravel roads. Capture mortality was <1.0%. We recorded low mortality (4.6%) up to 2 weeks post capture that may have been attributed to capture and handling stress. This technique proved effective at capturing greater sage-grouse and we believe this method can be effective at capturing other lekking species of prairie grouse with similar behavioral traits.

2.2 Introduction

Sage-grouse (*Centrocercus* spp.) have been the subject of numerous research projects in the western United States and Canada (Knick and Connelly 2011). Greater sage-grouse (*C. urophasianus*; hereafter sage-grouse) were listed as “warranted but precluded” in 2010 under the 1973 Endangered Species Act (as amended; USFWS 2010). However, on October 2, 2015 sage-grouse were removed from consideration of being listed as threatened or endangered; their status will be reviewed again in 2020 (USFWS 2015). Because sage-grouse continue to be a species of conservation concern, research requiring trapping and marking of sage-grouse will likely continue.

Common capture techniques for sage-grouse include rocket/cannon-netting (Lacher and Lacher 1964), drop-netting (Giesen et al. 1982, Bush 2008), walk-in traps (Schroeder and Braun 1991), and spotlighting (Wakkinen et al. 1992). These techniques have been widely used and have proven effective for capture in many areas, but each method has limitations and associated costs (Lacher and Lacher 1964, Giesen et al 1982).

The most widely used method for capturing sage-grouse is spotlighting from truck, all-terrain vehicle (ATV), or on foot (Giesen et al. 1982, Wakkinen et al. 1992). Spotlighting (sometimes termed night-lighting) involves locating sage-grouse at night with a spotlight and capturing them with a hoop net. This technique has proven successful in many areas (Holloran et al. 2005, Kirol et al. 2012), yet has had limited success in sparsely populated areas and when few grouse roost on or near a lek (B.L. Walker, Colorado Division of Parks and Wildlife, personal communication). Also, researchers studying the same population for multiple years have noted that sage-grouse seem to become progressively more difficult to capture using spotlighting, possibly because individuals become acclimated to the technique (M. J. Holloran, Operational Conservation LLC, personal communication). Spotlighting can only be done at night, working through the night several nights in a row is exhausting for technicians and presents logistical and safety challenges. Spotlighting is also less effective on nights with substantial lunar illumination, in high winds, and when it is snowing (B.L. Walker, Colorado Division of Parks and Wildlife, personal communication).

Rocket/cannon-netting involves deploying a large net (e.g., 36.5 m long x 12.2 m wide) on an area where sage-grouse concentrate, generally a lek. Black powder charges detonate projectiles attached to the net carrying it over the target. Rocket/cannon-netting can result in injuries or mortality of the targeted species, and disrupt breeding behavior if employed on a lek (Silvy et al 1990). Rocket/cannon-netting can also be dangerous to the capture crews and presents a fire hazard due to the use of black powder charges (Silvy et al. 1990; A.L. Sutphin and T.E. Maechtle personal observation). A rocket/cannon net can take up to 2 hr to set up with 4-6 individuals (Moynahan et al 2006; A.L. Sutphin and T.E. Maechtle personal observation). In addition, with rocket/cannon-netting, investigators capture nontarget grouse, for example capturing males, when females are the focal sex. Working with black powder charges presents significant logistical challenges. Black powder charges need to be stored and handled under strict safety protocols. Additional challenges exist relating to misfires, fire hazards, special permitting in most jurisdictions, and shipping (Silvy et al. 1990, B.L. Walker, Colorado Division of Parks and Wildlife, personal communication). Giesen et al. (1982) attempted to capture sage-grouse using rocket/cannon net mounted on the front of a truck and noted safety concerns regarding detonations within the vehicle. They had minimal success (6% of captures) and approximately half of the sage-grouse captured sustained broken wings.

Drop-netting involves a net that is erected above a lek and supported by poles; once sage-grouse are under the net, a rope is pulled dropping the net (Leonard et al. 2000). Drop-netting is a useful means of trapping sage-grouse in some areas (Bush 2008), but is infrequently used because setup can be complex and time consuming, individual birds cannot be targeted, and individuals often move lekking activities from under the stationary nets after they are erected (Connelly et al. 2003; K.T. Smith, University of Wyoming, personal communication). The final traditional method of sage-grouse capture is walk-in traps that are typically set up on or near leks to capture prairie grouse with have a funnel-shaped opening where birds can enter but not easily exit the trap (Schroeder and Braun 1991, Aldridge and Brigham 2002, Smith 2010). Walk-in traps are also time consuming to set up and are generally less effective at capturing birds than other methods (B.L. Walker, Colorado Division of Parks and Wildlife, personal communication).

We describe a mobile capture technique for sage-grouse. We modified a net launcher for mounting on a vehicle and used the technique to capture sage-grouse in northeastern Wyoming, USA. The mobile net launcher addresses concerns associated with the other methods described by minimizing injuries, reducing set-up time and difficulty, minimizing disturbance of lekking activities, allowing for targeting of specific individuals, and providing mobility. Together these benefits increased capture of birds in areas with low population densities, and allowed for capture during daylight.

2.3 Methods

2.3.1 Study area

Our research occurred in the Powder River Basin (PRB), primarily in Johnson County with the northern portion extending slightly into Sheridan County, Wyoming (106°20'2.538"W, 44°18'35.431"N). The study area encompassed 937-km^2 of which 61% was private land, 33% public land administered by the U.S. Bureau of Land Management, and 6% Wyoming state land. Cattle and sheep ranching were the primary agricultural uses and energy development, predominantly in the form of coal bed natural gas, was the primary energy extraction activity occurring in the study area. The study area was within the Great Plains Sage-Grouse Management Zone, which included part of the Powder River sage-grouse population and provided year-round habitat for sage-grouse (Doherty et al 2008, USFWS 2010, Fedy et al. 2015, Kirol et al. 2015*b*). The climate in the study area was semi-arid. Monthly average temperatures ranged from 21.6° C in the summer to –5.8° C in the winter. Annual precipitation averaged 33 cm to 43 cm and average annual snowfall ranged from 84 cm to 170 cm. The majority of the study area was shrub-steppe habitat dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*). Plains silver sagebrush (*A. cana cana*) was present, but at much lower abundance and is limited to drainage corridors.

2.3.2 Materials

The CODA Net launcher (CODA Enterprises, Mesa, AZ, USA; hereafter net launcher) uses expanding gas from a blank .308 caliber rifle cartridge to propel 4 projectiles (~300 g/projectile) attached to a net that rests in a fiberglass canister. An electronic detonator activates the net launcher and deploys the net. Four projectiles are propelled from 4 barrels and carry the net over the target. The barrels are easily adjusted or removed with a wrench and the net launcher can be set up by one person in <5 min. The net must be folded accordion-style to deploy correctly.

The Bureau of Alcohol, Tobacco and Firearms (ATF) of the U.S. Department of Justice determined the net launching device was not designed as a weapon and is not readily converted to a weapon. Therefore, it is not subject to the provisions of the Gun Control Act (GCA) (Bureau of Alcohol, Tobacco and Firearms, Washington, D.C. 20226, October 30, 1981, File # T:T:F:CSL 7540). This allows for interstate transportation and shipping without restriction.

Figure 2.1: Bumper-mounted CODA (CODA Enterprises, Mesa, AZ, USA) net launcher side view and dimensions, which was used to capture greater sage-grouse in Wyoming, USA, during spring and autumn 2008–2011.

From 2008 to 2011, we used the net launcher (Figure 2.1) to capture sage-grouse in the PRB in Wyoming. We used the device to capture sage-grouse near leks in the mornings (≥200 m from lek center) during the breeding season and along roadways later in the year, both at dusk and dawn. Although the net launcher has been used as a stationary unit to capture sage-grouse on leks (Hausleitner 2003); we modified the unit to be mounted to the front receiver of a truck or ATV to make it mobile (Figures 2.2 and 2.3). We welded 5.08-cm steel square tubing to the net launcher and welded a 5.08-cm hitch receiver to the front of a truck or ATV. The receiver protruded 5 cm beyond the front of the truck or ATV and remained parallel to the ground. The steel square tubing was inserted into the receiver and secured with a receiver pin. (Figure 2.1). We used a 9.14-m x 9.14-m net with 5.08-cm mesh in the net launcher. Net launchers ranged in cost from US$3600.00 to $4300.00, and a box of 100 blank .308 cartridges cost US$105.00. Costs of welding labor and materials varied depending on regional differences in labor costs (we paid < $100).

2.3.3 Spring captures

Sage-grouse females around lek perimeters (both from roads and fields) that were not interacting with males were targeted for capture from 1 hr before to 3 hr after sunrise. Once positively identified, the vehicle operator attempted to keep the grouse in front of the vehicle while the passenger controlled the detonator switch (with ATVs, one person controlled both the vehicle and the detonator). Females were approached at ≤20 km/h and kept directly in front of the truck or ATV. Once females were in range (5-8 m), the driver and passenger released anchor weights (dropped from their hands out of the truck windows) secured to the back of the net, followed immediately by detonation of the net launcher and deployment of the net. Following capture, sage-grouse were restrained to minimize risk of injury by quickly removing them from under the net for processing and release. If multiple grouse were captured, each individual was placed in a cardboard box until they were processed.

Figure 2.2: Bumper-mounted CODA (CODA Enterprises, Mesa, AZ, USA) net launcher on pickup truck. We developed this method to capture greater sage-grouse in Wyoming, USA, during spring and autumn 2008–2011.

Figure 2.3: Bumper-mounted CODA (CODA Enterprises, Mesa, AZ, USA) net launcher on ATV. We developed this method to capture greater sage-grouse in Wyoming, USA, during spring and autumn 2008–2011.

2.3.4 Late summer/fall captures

Sage-grouse do not congregate on leks in the fall, so during late summer and fall we used a different approach to capture sage-grouse. We slowly drove along dirt roads at dusk and dawn in sage-grouse habitat with the net launcher mounted on the vehicle or ATV. We chose to search for grouse at dusk and dawn as they are more active during these time periods and likely to be in the open. Once we located one or more females in an accessible area, we followed the same procedures described above. We stayed on roads and borrow ditches to minimize habitat disturbance.

2.3.5 Use of a herder

Similar to other trapping techniques (Giesen et al. 1982), attempting to move birds into areas where the likelihood of capture is greater (i.e., herding) could increase capture success with the net launcher. In our study, herders sometimes drove an ATV or a truck, whereas at other times they were on horseback or on foot. Grouse that were calm and not paying particular attention to the vehicle could often be herded whereas hens that frequently looked at the vehicle or quickly walked out of reach were likely to flush. Herding proved effective at moving birds out of areas with a high density of sagebrush or other areas where the net launcher was not as effective.

The Wyoming Game and Fish Department issued a Chapter 33 Permit for this research and the researchers who directed trapping and monitoring of sage-grouse were trained under the Animal Care and Use Protocol of the University of Montana when working on previous sage-grouse research in the PRB (e.g., Doherty et al. 2008). This same protocol was followed when conducting this research.

2.4 Results

During our 4-year study, we focused on capturing female sage-grouse and captured 92 sage grouse (82 captures of ≥1 grouse in 115 attempts, 71%) using the net launcher, including 30 adult females, 57 yearling females, 3 hatch-year females, and 2 adult males. The mean number of grouse caught per successful attempt was 1.30 (give range). Capture success was 69% and 71% for morning and evening capture attempts, respectively. We attempted 70 captures in the spring and 45 captures in the fall. Capture success in both seasons was 71%. Mortality and injuries associated with capture were low. One captured sage-grouse sustained a broken wing and had to be euthanized, but no other birds were injured. We conducted biweekly monitoring of 87 females captured with the net launcher. Four of the 87 females died from unknown causes within 4 weeks after capture (95% survival).

Of our 33 unsuccessful capture attempts, we were unsuccessful in our capture efforts due to poor net deployment during 4 capture attempts. In these cases, the net was either folded incorrectly or debris was entangling the net. On 2 separate occasions, sage-grouse walked out from under the net that was held up by shrubs. Wind (>24 km/hr) adversely affected net deployment on 4 capture attempts resulting in failed attempts as the net was blown off-target. Slope of the ground (>10°) was responsible for 3 failed capture attempts. On 2 occasions, we attributed failure to repetitive attempts on the same flock of females on the same capture day, although this is hard to determine conclusively and could have been the cause for numerous other failures. Other failed attempts (*n* = 18) were due to hens quickly escaping to the side or front of the net before it contacted the birds.

2.5 Discussion

Our mobile net launcher resulted in high capture rates and caused minimal mortality or injury of sage-grouse. This method is likely most useful in areas of low sage-grouse density in which spotlighting can be time consuming and less effective (B.L. Walker, Colorado Division of Parks and Wildlife, personal communication). The approach we present addresses 2 of the main goals of animal capture in that it minimizes effects on the species and maximizes capture success. The effectiveness of our capture approach can be influenced by a number of factors, but overall, provides many advantages over alternatives.

Researchers can maximize the probability of successful captures by considering factors that influence the net launcher effectiveness. High cross or head winds (≥24 km/hr) prevented bird capture and we concluded that in winds ≥ 24 km/hr, we needed a tail wind or we would not attempt captures. Giesen et al. (1982) also noted that wind adversely affected the deployment of their vehicle-mounted cannon net. As in most avian capture approaches we advise against capture attempts during precipitation events as the moisture will increase the weight of the net and handling birds in snow or rain can be unduly stressful for the species. Terrain, particularly slopes greater than 10°, can affect net deployment by causing the net to shift with the slope. Thus, when positioned on a side slope the vehicle should be oriented to fire higher on the slope than the target individuals as the net will drop with the contour of the land. Time of day and season had no apparent influence on our success rates. However, we did not attempt mid-day captures as grouse were typically in thick sagebrush and thus, out of reach of the net launcher. Finally, the net must be folded properly and kept clean of debris such as twigs and pieces of vegetation to ensure successful deployment.

Biotic factors, including bird behavior, and habitat structure can also influence capture success. Woody vegetation (e.g., sagebrush) prevents the net from completely collapsing over the target. During our research, grouse walked out from under the edges of nets suspended on sagebrush on 2 occasions. Nonwoody vegetation such as grasses and forbs did not adversely influence our capture success. Bird behavior, flock size, and capture history (i.e., previous attempted capture on grouse) also affect capture success. Multiple capture attempts in the same area may result in birds becoming habituated. Researchers should be aware of species-specific behavioral cues that indicate probable flushing and unsuccessful capture attempts. If the researchers can predict the direction of flush, it is advisable to 'lead' the birds when deploying the net launcher. Foraging birds that displayed minimal vigilance in response to the approaching vehicle were easier to capture. We suggest captures of 3 or fewer sage-grouse per attempt because larger groups are harder to capture due to group vigilance and to reduce the potential for injury. Attempting captures on multiple birds can also lead to injury from the net projectiles (the metal weights that carry the net over the target) striking the birds.

The mobile net launcher approach we describe here presents a number of advantages when compared to alternative common capture approaches. These advantages include greater targeting precision and trapping efficiency, and lower disturbance and injury. The mobile net launcher allowed investigators to be selective, reducing disturbance of non-target individuals. In contrast, rocket-nets and drop-nets are both stationary capture methods and less selective. Trapping efficiency was increased due to lower set up time compared to much more labor intensive approaches (Connelly et al. 2003, Walker 2008).

The mobile net launcher decreased disturbance by allowing us to focus our capture efforts on the periphery of leks (≥200 m) as compared to drop-netting (Giesen et al. 1982, Bush 2008), rocket-netting (Lacher and Lacher 1964), and walk-in traps which are typically set-up directly on leks (Schroeder and Braun 1991). Additionally, we had only one serious injury in 92 total captures. Rocket-netting can result in a higher proportion of injuries and deaths to the target species (Silvy et al.1990). Sell (1979) suggested not using rocket-nets on lesser prairie-chickens (*Tympanuchus pallidicinctus*) because of the high likelihood of injuries and deaths with this method. Haukos et al. (1990) reported that injuries to lesser prairie-chickens with walk-in traps can be higher than rocket-netting. Schroeder and Braun (1991) stated that greater prairie-chickens (*T. cupido*) were in walk-in traps for 30-45 min prior to extraction and 8 of their 231captures resulted in death. Birds in traps can be susceptible to predation or sustain injuries from the chicken wire due to attempted escapes, or fighting over territories in a confined space (Haukos et al. 1990, Schroeder and Braun 1991). Overall, survival was high post-capture and comparable to Hausleitner

(2003) who documented 96% survival in the first month post-capture on 26 sage-grouse captured using a stationary net launcher and 90% survival of 116 grouse captured using spotlighting techniques. The net launcher caught a comparable percentage of yearling birds when compared to rocket netting, suggesting the approach is not biased towards capture of young birds (Doherty 2008). Although our capture efforts focused on females, similar behavioral responses during previous capture efforts and on-going research on males (B.C. Fedy and C.P. Kirol personal observation) suggest this method would be effective on males as well.

Our mobile net launcher is only appropriate for species that are approachable by vehicle. Sage-grouse are easily approached by vehicle and more to likely flush when approached on foot. Sharp-tailed grouse (*T. phasianellus*) are also approachable by vehicles while they are on their breeding grounds and thus, are potentially susceptible to capture with our approach (B.C. Fedy and C.P. Kirol personal observation). Cope (1992) reported that capture success using spotlighting was limited for sharp-tailed grouse in British Columbia, Canada. Other capture methods such as rocket-netting can yield greater numbers per attempt compared to the net launcher, but also capture non-targeted birds. We typically captured 3 or fewer birds per attempt with the net launcher, compared to 30 hens in one attempt with the rocket-net. Although, Haukos et al. (1990) reported capturing 2 or fewer lesser prairie-chickens on most attempts using rocket-nets.

Our research suggests that the vehicle-mounted net gun described here is an effective technique to capture sage-grouse while reducing handling time, injury, and stress-related mortality to targeted and non-targeted individuals. This holds true especially in areas of low sage-grouse densities where other methods prove less effective. Based on our trapping experience, we feel that this method could be effective for capturing other lekking grouse species such as Gunnison sage-grouse (*C. minimus*) and sharp-tailed grouse.

Chapter 3

Coupling tracking technologies to maximize efficiency in avian research

3.1 Abstract

Direct marking and tracking of wildlife using telemetry is widespread and critical to understanding many aspects of wildlife ecology. For most species, researchers must select between multiple tracking technologies that represent trade-offs among data requirements, mass, and cost. Options tend to be more limited for smaller, volant species. We developed and tested a unique combination of a store-on-board Global Positioning System logger with an independent very-high-frequency (VHF) tag (hereafter hybrid tag) fitted on the greater sage-grouse (*Centrocercus urophasianus*) with a modified harness design in northeastern Wyoming, USA, 2017-2018. We compared hybrid tags with other tracking technologies commonly used in avian research, namely VHF and Argos satellite relay tags. Given our research objectives, that required both frequent location data and field-based observational data, we found the hybrid tags were the most cost-effective option and capable of collecting more location data compared with Argos tags because of power savings associated with data transmission. Cost savings allowed us to avoid sacrificing sample size while still obtaining high-resolution location data in addition to field-based observational data such as the presence of chicks. We believe our hybrid tags and harness design would be beneficial to research on other avian species of comparable size to the greater sage-grouse and those that are relatively localized year-round, including many other Galliformes.

3.2 Introduction

Wildlife ecology has a long history of using biotelemetry to track and study animals. Very-high-frequency (VHF) tags were first designed and tested for animal studies in 1959 (LeMunyan et al. 1959) and have been critical tools to understanding many aspects of species ecology. More recently, biotelemetry technologies using internal GPS (Global Positioning System) to collect high-resolution location data have become widely available. Technological advancements have reduced effects on telemetered animals, increased data availability and reliability, and decreased costs. Reductions in the mass and size of transmitters and improved attachment methods, have opened up opportunities for researching small animals and, particularly, those that fly. With a variety of telemetry systems now available, selecting the most appropriate system for a study requires careful considerations of tradeoffs associated with different technologies and study objectives (Hebblewhite and Haydon 2010, Thomas et al. 2011, Taylor et al. 2017).

Sage-grouse (*Centrocercus* spp.) are one of the most extensively researched species in North America and the first birds were fitted with VHF radiotransmitters in 1965 (Eng and Shladweiler 1972). Since then, researchers have tested various telemetry devices and configurations as well as attachment methods on sage-grouse. Consequently, this species provides valuable information on implementation of new and old tracking technologies and attachment methods that are applicable to many less-studied avian species.

When attaching a telemetry device (hereafter tag) to an animal, careful consideration of the ratio of mass of the tag to the body mass of the study species is necessary (Aldridge and Brigham 1988, Samuel and Fuller 1994, Fair et al. 2010). Tag options are more limited for small, volant species (Barron et al. 2010). Research on volant species fitted with tags has shown that the additional mass of the tag can affect flight patterns and increase energetic costs (Barron et al. 2010, Vandenabeele et al. 2012). Although there is not a consensus on a specific tag-to-body mass ratio that is appropriate for all volant species (e.g., 3% or 5%), there is a general consensus that detrimental effects are reduced with proportionally lighter tags (Fair et al. 2010, Vandenabeele et al. 2012). The earliest VHF tags fitted on sage-grouse weighed 70 grams, had a battery life of less than a month (Kenward 2001, Connelly et al. 2003). By the late 1970s, mass of VHF tags commonly used on sage-grouse were reduced to 25 g (~2% of the mass of an adult female) and the battery life was extended to ≥6 months (Connelly et al. 2003).

Researchers require secure attachment of tags that does not harm the animal or affect the animal in ways that may cause systematic bias in the data (Barron et al. 2010). Over the past 50 years, sage-grouse researchers have experimented with a variety of attachment methods including neck-mounted poncho and necklace tags, backpack tags secured around the wings, and rump-mounted tags secured around the legs (Connelly et al. 2003, Bedrosian and Craighead 2010). Tags secured around the neck of the sage-grouse (hereafter VHF necklace) have become the most commonly used tag and currently weigh between 17 and 22 g with a lifespan of approximately 2 years (Frye et al. 2014, Dinkins et al. 2016, Walker et al. 2016).

More recently, satellite relay (Argos; www.argos-system.org), GPS solar-powered Platform Transmitter Terminal (PTT) tags fitted to sage-grouse using a rump-mount harness system has become a more common used tool (Bedrosian and Craighead 2010, Dzialak et al. 2011, Hansen et al. 2014, Smith et al. 2016). Argos PTT tags weigh between 22 and 30 g (Dzialak et al. 2011, Hansen et al. 2014, Smith et al. 2016, Pratt et al. 2017) with approximately 10 additional grams in harness and attachment materials (Pratt et al. 2017). These light-weight Argos PTT tags gather and transmit GPS data via Argos satellites and are powered by batteries that recharge by solar panels (Thomas et al. 2011). The solar panel is positioned on top of the Argos unit, so these tags are fitted on the back of the grouse as a rump-mount to allow for direct sunlight to charge the battery. Unlike a backpack-style harness, the rump-mount method places the tag dorsally on the rump of the bird and the harness material is secured around the legs rather than the wings (Bedrosian et al. 2007, Smith et al. 2016).

The purchase cost of Argos PTT tags are approximately 20 times greater than VHF tags and costs of Argos systems increase with the download frequency because of satellite data download fees (Hebblewhite and Haydon 2010, Thomas et al. 2011, Hansen et al. 2014). Argos PTT tags collect a large amount of location data at frequent intervals and, in general, do not require a researcher to visit study sites to track the animals (Hebblewhite and Haydon 2010, Kays et al. 2015). However, research budget restraints and high cost of Argos PTT tags often limits the number of study animals that can be marked, which may influence statistical power and capacity of the marked population to represent the larger population of interest (Hebblewhite and Haydon 2010). The comparatively low-cost VHF units allows for larger numbers of marked birds given the same budget, and are well-suited for gathering data that require field-based observations such as nest success or brood size (Hebblewhite and Haydon 2010, Kirol et al. 2015*a*). Yet, location data obtained from VHF tags are labor-intensive, infrequent, and prone to human error and may also be constrained by limits on access due to weather, road conditions, or land ownership (Withey et al. 2001, Hebblewhite and Haydon 2010, Gerber et al. 2018). Sage-grouse studies using VHF tags usually track and collect locations for individual birds once or twice per week (Fedy et al. 2012, Walker et al. 2016). Conversely, sage-grouse studies using Argos PTT tags have collected >9–15 locations/day (Dzialak et al. 2011, Smith et al. 2016, Pratt et al. 2017, Foster et al. 2018).

In practice, the most appropriate tracking technology for a given study is highly dependent on the study objectives, which dictate factors such as required sample size, sampling rate, and precision of locations needed. Yet, many studies have the goal of population-level inference over large landscapes, and require precise and frequent location data to quantify space use and movement patterns, but may also need observational data to assess population fitness rates (e.g., nest success). In these cases, tradeoffs between GPS satellite tags and VHF tags are substantial. A hybrid technology that eliminates some of these tradeoffs would be beneficial to many studies that require both frequent location data and field-based observational data. We assessed the functionality of a new approach to tracking sage-grouse that provides frequent and accurate GPS locations, at a cost that does not severely limit sample size, and allows for field-based observational data. Specifically, we required tags that would 1) allow for a sample of ≥40 individuals, 2) cost <US$100,000 (≤US$2,500/unit), 3) have a life span of ≥2 years, 4) provide accurate GPS location data across seasons, 5) provide frequent GPS locations throughout a 24-hour period, 6) weigh <3% of body mass (Fair et al. 2010), and 7) allow real-time tracking in the field to gather observational data. In addition to these considerations, we wanted to ensure we could recover tags if they stopped transmitting for any reason (e.g., malfunction, power loss, damage due to depredation).

We developed and tested a unique combination of a store-on-board GPS logger with an independent VHF tag (hereafter hybrid tag) to meet our research requirements. We detail a hybrid tag we developed and assessed its capacity to meet project goals and outcomes. Specifically, we present 1) the utility of the combined GPS logger and VHF tag, 2) a cost comparison among Argos PTT tags, VHF necklace tags, and hybrid tags, 3) realized benefits of the VHF add-on with an independent battery, and 4) our modified harness system to reduce effects of attaching a rump-mounted tags to greater sage-grouse (Centrocercus urophasianus).

3.3 Methods

3.3.1 Study area

Our study was in the Powder River Basin, primarily in Johnson County with the northern portion extending into Sheridan County, Wyoming, USA. The area was characterized by rugged terrain bisected by deep drainages with prominent hogback ridges, knolls, and escarpments. The majority of the study area was shrub-steppe habitat dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*). The climate in the study area was semiarid. Monthly average temperatures ranged from 21.6° C in the summer to −5.8° C in the winter. Annual precipitation averaged 33 cm to 43 cm and average annual snowfall ranged from 84 cm to 170 cm. More details on study area characteristics are available in Fedy et al. (2015).

3.3.2 Field methods

We captured female sage-grouse in 2017–2018 using spot-light and hoop-net methods (Giesen et al. 1982) and a mobile CODA net launcher (Sutphin et al. 2018). We fitted females with rump-mounted 13-g solar LRD (long range download) GPS-UHF (ultra-high frequency) tags (Harrier-L; Ecotone Telemetry Lech Iliszko, Sopot, Poland) combined with independent 10-g VHF tags (RI-2B; Holohil Systems Ltd, ON, Canada). Only females that weighed >1,000 g were fitted with hybrid tags. We deployed tags with approval from the University of Waterloo (Animals for Research Act and the Canadian Council on Animal Care guidelines, AUPP# 16-06).

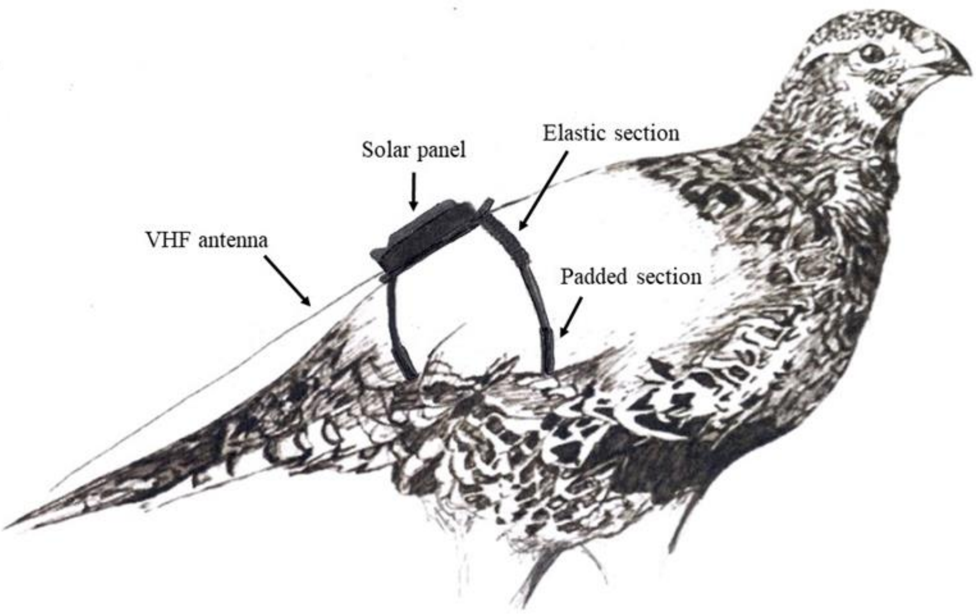
We monitored tagged female sage-grouse weekly from April through August and bimonthly throughout the winter (Sep–Mar). We tracked females using the VHF signal with a R-1000 hand-held receivers and 3-element Yagi antennas (Communication Specialists, Orange, CA, USA) and downloaded the GPS data from GPS loggers using mobile UHF base stations and unidirectional antennas (Ecotone Telemetry Lech Iliszko). Radio activity intervals can be programed to 1, 5, or 10 minutes. We programed our GPS loggers to attempt to communicate (i.e., radio activity interval) every minute. The manufacturer of the GPS loggers (Harrier-L) suggested managing the power at a voltage >3.7. The GPS loggers were originally programed to collect GPS locations every 4 hours (6 locations/24-hr period) and maintained high voltage. The transmitters maintained high voltage when set to collect a location every 4 hours; therefore, we transmitted new settings to the loggers instructing that they record GPS locations every 30 minutes (48 locations/24-hr period), in late-summer 2008. The GPS loggers require line-of-sight for communication and download. The rough terrain in our study area dictated that we commonly had to be within ≤300 m of the female to establish line-of-site communication with the GPS logger. On occasion, if there was rock outcrops or thick vegetation obstructing line-of-site communication, we needed to get much closer than 300 m to download stored data. We used VHF tracking to isolate tagged females to a particular draw or sagebrush patch. After isolating the bird, we pointed the UHF antenna in the direction of the VHF signal and attempted to download the GPS data. If we failed to establish communication with GPS logger, we continued to track the bird and attempted to download again from a different position. We used tablet computers to power the base station, which also allowed us to visually confirm communication with GPS loggers, view location data, and adjust logger settings in the field, when needed. The base stations can be powered by any power source that has a USB port, such as cell phone boosters. The tablets allowed for real-time monitoring because we could view the GPS logger data using Google Earth (Google LLC, Mountain View, CA, USA) software while tracking. After we downloaded the GPS data from the logger, we maintained a distance of ≥50 m from the tagged sage-grouse unless we needed to visually confirm reproductive state or survival. In those cases, we downloaded the GPS data before we attempted to observe the bird. During the nesting period (mid-Apr–Jun) we used VHF tracking to approach within ≥20 m of the female to verify nesting. Once we confirmed a female was on a nest by getting a visual with binoculars, we monitored her and downloaded data weekly from ≥50 m until she was no longer on the nest. If the GPS data showed that a female was on a nest for the entire incubation period (26–28 days), we verified nest survival (i.e., nests with ≥1 hatched egg) by examining eggshells and other diagnostic signs

(Wallestad and Pyrah 1974). Following a successful nesting effort, we attempted to get a visual of the female every second week to confirmed chick presence by visually locating chicks with binoculars or observing brooding behavior by the female (e.g., distraction displays, feigning injury, and clucking). We confirmed brood fate at approximately 35 days posthatch by VHF ground-tracking at night and conducting spotlight counts (Dahlgren et al. 2010). We confirmed brood survival at 35 days posthatch because the majority of chick mortality has already occurred by this age; consequently, chicks alive at 35 days are more likely to survive to breeding age (Gregg et al. 2007). We considered a brood to have survived if we observed ≥1 chick during spotlight counts (Kirol et al. 2015*a*).

We located nests that were initiated early or failed quickly, and not found during VHF ground-tracking, by using the GPS data downloaded from the female's tag to identify clusters of points suggesting a nest attempt. We then surveyed these areas to verify a nesting attempt. If we were tracking a female and suspected that she may have died, we would download and view the GPS data to determine whether the logger was stationary for an extended period of time. When GPS data suggested that the tagged sage-grouse was not moving, we would track the bird to conclusively assess fate and document any diagnostic evidence at mortality locations.

3.3.3 Technology and equipment

Hybrid tags were fitted on sage-grouse with custom-made harnesses. Our harness design allowed for expansion to accommodate growth and reduced abrasion along the inside of the legs (Figure 3.1). We made the harnesses from 0.64-cm tubular Teflon (Chemours, Wilmington, DE, USA) ribbon with 0.64-cm elastic inserted within the ribbon to provide for expansion. We cut the Teflon ribbon to 70 cm and cut the elastic insert to 6.5 cm. We placed marks on the ribbon at the center and at 5.0 cm on either side of the center. We used fine wire to pull the cut pieces of elastic into the ribbon. We stitched the elastic in place at one of the 5.0-cm marks with strong thread. We then used the wire to pull the elastic tight and bunch up the ribbon until the other end of the elastic reached the second 5.0-cm mark. We stitched the elastic in place at the second mark and removed the wire (Figure 3.2). This allowed the center of the harness to flex with the elastic insert.



Sketch by Megan Wilcox

Figure 3.1: The tag (hybrid tag) positioned dorsally at the rump (rump-mounted) of a female sage-grouse northeastern Wyoming, USA, 2017–2018. The harness is secured snugly around the legs between the abdomen and the thigh (the harness in curved in the sketch to show how it forms around the grouse's body).

After retrieving rump-mounted tags from sage-grouse during earlier research, in some instances, we would find abrasions and scabbing under the legs that we suspected were caused by the tubular Teflon material folding onto itself and bunching under the legs. To provide padding and some rigidity to the tubular webbing and prevent the ribbon from folding over, we cut strips of 4-mm-wide pieces of 3-mm neoprene (L Foam Neoprene Fabric; Rockywoods Fabrics, Loveland, CO, USA) to a length of 10 cm. We used needle and thread to pull the pieces of neoprene through the tubular webbing. When the neoprene strip was approximately 4 cm from the elastic stitch mark, on each side of the harness, we pulled the needle through the outside of the webbing and stitched the neoprene in place. This secured the 10-cm neoprene segment within the portion of the harness that runs between thigh and abdomen (Figures 3.1 and 3.2). Once the harness was adjusted to the bird, we secured it with approximately 0.64-cm- (one-quarterinch) diameter copper tubing cut into 0.64-cm-wide rings. We crimped the copper rings on the harness near the back loops of the tag to hold the harness in place (Figures 3.2 and 3.3).

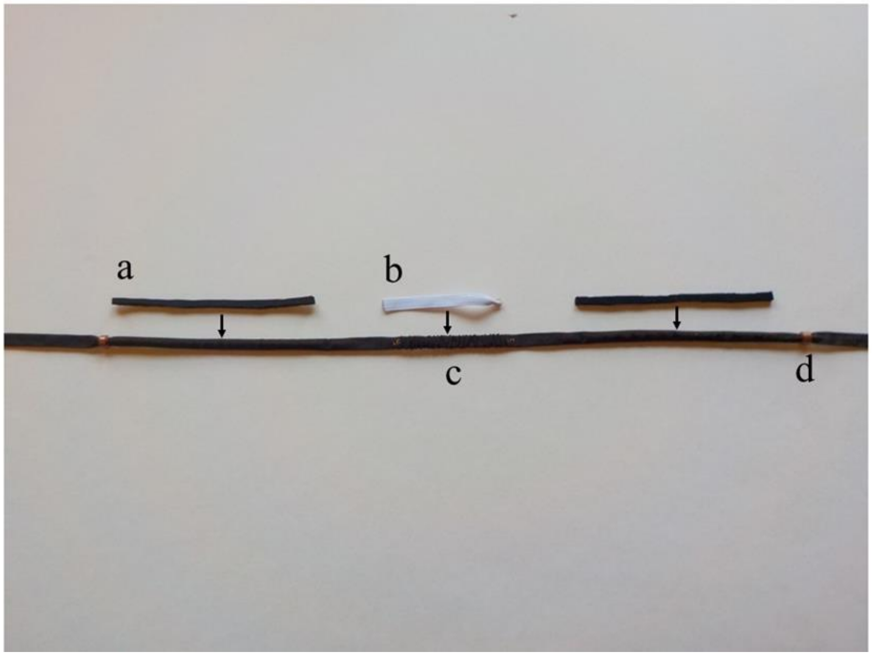


Figure 3.2: Components of the harness used to fit the rump-mounted tag (hybrid tag) on a sage-grouse. The pieces of 4-mm-wide 3-mm neoprene were cut to a length of 10 cm (a), inserted into the tubular Teflon ribbon, and stitched in place 4 cm from the elastic stitch marks. The 6.5-cm length of elastic (b) was inserted within the ribbon and stitched at 5-cm marks on each side of the center of the harness. The center of the harness, with the elastic insert, was bunched up between the 5-cm stitch marks to allow the center of the harness to flex with the elastic. The harness was secured on the sage-grouse by crimping approximately 0.64-cm-diameter (1/4 inch), 0.64-cm-wide rings made from copper tubing.

Figure 3.3: Hybrid tag fitted on a female sage-grouse in northeastern Wyoming, USA, 2017–2018.

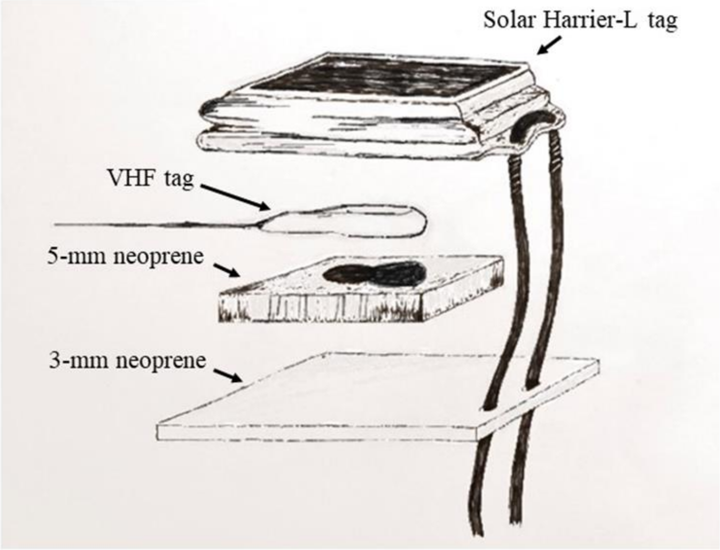


Figure 3.4: The components of the hybrid tag fitted on sage-grouse. The very-high-frequency (VHF) tag (RI-2B; Holohil Systems Ltd, ON, Canada) was centered and glued to the base of the Global Positioning System (GPS) logger (solar Harrier-L [long range download] GPS–UHF [ultra-high frequency]; Ecotone Telemetry Lech Iliszko, Sopot, Poland). The piece of 5-mm neoprene, with a cut out of the VHF outline, is glued to the base of the logger with the VHF nested within the neoprene. A piece of 3-mm neoprene is then glued to the bottom and the harness ribbon is threaded through the holes in the neoprene.

We attached the VHF underneath the GPS logger, rather than on the side, to keep the center of gravity over the middle of the sage-grouse laterally to reduce any potential impact on flight (Caccamise and Hedin 1985, Bedrosian and Craighead 2010). The dimensions of the VHF tag (L 40 × W 23 × H 5 mm) allowed the VHF to easily fit underneath the base of the GPS logger (L 60 × W 26 × H 14 mm; Figures 3.4). When building the hybrid tags, we first centered the VHF unit and glued it to the base of the logger. We then cut a piece of 5-mm neoprene to the dimensions of the GPS logger base and cut out the outline of the VHF within the piece of neoprene. We then glued this piece of neoprene to the base of the GPS logger with the VHF nested within the neoprene (Figures 3.4). We then glued a piece of 3-mm neoprene padding cut to 70 mm long and 40 mm wide onto the underneath side of the hybrid tag and completely covered the VHF tag. We cut this piece of neoprene to protrude 10 mm beyond the front and 7 mm on each side of the tag to act as a feather shield to prevent feathers from shading the solar panel. We made 2 holes in the front of this piece of neoprene to allow the harness to thread through the neoprene and front logger loops (Figures 3.3 and 3.4).

Based on concerns outlined in Bridge et al. (2011), we attempted to minimize aerodynamic drag by keeping the profile above the back of the hybrid tag as low as possible and positioning the VHF antenna parallel to the tail (Figure 3.1). Unlike Argos PTT tags, the GPS loggers did not have an antenna protruding out of the back of the unit.

3.3.4 Cost comparison

Estimating the net cost per datum of different tracking technologies has been shown to be a valid way to compare costs of different tracking technologies (Thomas et al. 2011). We compared costs per datum based upon the objectives of our study that required both location data and reproductive state information. Through the collective experience of the authors of this paper, we have used all of the tracking technologies being compared in this cost comparison while researching sage-grouse (Kirol et al. 2015*b*, Shyvers et al. 2019) We used realized costs from previous research and our current research project to provide a cost comparison per datum between VHF necklace tags (Fedy et al. 2015, Kirol et al. 2015*b*), Argos PTT tags (Hansen et al. 2014, Smith et al. 2016, Shyvers et al. 2019), and the hybrid tags used in this study. We standardized cost comparison across technologies based on marking and tracking 30 female sage-grouse for 4 months over a summer (May–Aug). To provide a conservative cost comparison of Argos technology, we assumed that sage-grouse fitted with Argos tags would require no tracking or monitoring in the field (i.e., no field visits) and satellite transmissions would occur on 5-day intervals. When using Argos technology, some field monitoring of the tagged sage-grouse might be necessary; however, some researchers have relied primarily on interpreting location and movement data to identify nesting attempts and reproductive state information (e.g., brooding or nonbrooding female sage-grouse) with few field visits (e.g., Webb et al. 2012). For VHF necklace tags, we assumed a twice per week ground-tracking would be needed. This is a common monitoring interval in VHF sage-grouse studies occurring during the reproductive season because some nest attempts—nests that are initiated early and fail quickly—can be missed when grouse are monitored less frequently (Walker et al. 2016). The cost comparison included all expenses related to each technology and, based upon our current and previous research, assumed that 2 research technicians would be required to track 30 sage-grouse fitted with hybrid tags once per week and 3 research technicians would be required to track 30 sage-grouse fitted with VHF necklace tags twice per week (Table 1). For instance, costs of 3 telemetry flights used to locate missing grouse that were fitted with VHF necklace and hybrid tags were included in the cost comparison.

Table 3.1: Cost estimates (USD) are for 30 female sage-grouse tagged with different technologies. Estimates are based on 4 months (May–Aug) of data collection. Cost estimates for very-high-frequency (VHF) necklaces (A4060; Advanced Telemetry Systems, Isanti, MN, USA) and tracking come from our previous research using these tags on sage-grouse (Fedy et al. 2015, Kirol et al. 2015*b*). Cost estimates for our hybrid tag (rump-mounted Global Positioning System [Solar GPS–UHF (ultra-high-frequency) tag, Harrier-L; Ecotone Telemetry Lech Iliszko, Sopot, Poland] fitted with a VHF [RI-2B; Holohil Systems Ltd, Ontario, Canada] add-on) come from our current study. All costs associated with field tracking and monitoring have been combined to provide a liberal estimate of costs. We derived cost estimates for the rump-mounted Argos tags (satellite up-link Argos, GPS Solar Platform Transmitter Terminal [PTT–100, Microwave Telemetry Inc., Columbia, MD, USA]) from previous sage-grouse research (Hansen et al. 2014, Shyvers et al. 2019). The estimates for the Argos tags assume that all data would come from remote data downloads and no field tracking would be necessary, northeastern Wyoming, USA, 2017-2018.

Tag type	Tags	Satellite download fee	Tracking equipment[a]	Tracking personnel[b]	Field transportation[c]	Telemetry flights[d]	Total
VHF necklace	$6,000	NA	$4,000	$29,520	$16,600	$4,500	$60,620
Argos PTT	$118,500	$6,872	NA	NA	NA	NA	$125,372
Hybrid tag	$48,000	NA	$6,500	$20,880	$14,400	$4,500	$94,280

[a] Tracking equipment for VHF tags included 3 receivers, 4 folding Yagi antennas, 3 personal GPS units, and $600 for miscellaneous and researcher safety equipment. Tracking equipment for the GPS logger–VHF included all the equipment listed above in addition to 2 UHF base stations, 2 unidirectional antennas, and 2 field tablets.

[b] For VHF necklace tags, requiring ground-tracking twice per week, we assumed that 3 researchers would be required to track 30 tagged sage-grouse. VHF necklace tag costs included hiring 3 research technicians and technician housing for 4 months. For Hybrid tags, that require ground-

tracking only once per week, costs are for 2 researchers to track 30 tagged sage-grouse. Hybrid tag costs included hiring 2 research technicians and technician housing for 4 months.

[c] Field transportation costs for VHF necklace tags, included 1 truck rental and 3 ATV rentals and fuel for 4 months of biweekly ground-tracking. Field transportation costs for Hybrid tags, included 1 truck rental and 2 ATV rentals and fuel for 4 months of weekly ground-tracking.

[d] On the basis of our current and previous research, we assumed that 3 telemetry flights would be required to locate missing grouse over a 4-month tracking season. Costs are for VHF tracking from a fixed-wing aircraft for 6 hours/flight.

We explored cost comparisons for 2 GPS logger sampling frequencies. First, given the inherent disparities in the frequency of location collection of the GPS units, we compared the cost per datum based on standard collection frequencies associated with each technology. We based the estimated costs on 35 locations (i.e., 5/day) for the Argos PTT and hybrid tags and 2 locations/week for VHF necklaces. An Argos PTT tag sampling frequency of 5 points/day is a standard sampling frequency in the summer for sage-grouse studies using solar Argos PTT tags that occurred at a similar latitude (e.g., similar solar energy potential; Pratt et al. 2017). For the second comparison, we used the highest collection frequency we found in the sage-grouse literature of 15 points/day for Argos PTT solar tags (Dzialak et al. 2011) and compared this frequency with the highest collection frequency used in our research of 48 points/day. We only needed to ground-track our hybrid tagged sage-grouse once per week in this study, so we used this monitoring frequency in our cost comparison. It is important to note, weekly ground-tracking is not necessary if the study intent is only to collect GPS locations because, according to the manufacture, the GPS loggers (Harrier-L) can store 30,000 GPS locations on board. In fact, projects using the same equipment on other species (e.g., northern goshawk [*Accipiter gentilis*]) are designed around encountering birds twice per year to download data (Blakey et al. 2020).

3.4 Results

Hybrid tags were fitted on 38 and 39 female sage-grouse in 2017 and 2018, respectively. The average body mass of the adult female (including first-year adults) sage-grouse was 1,428 ± 165 g. The GPS logger–VHF units (including the harness), weighed 29 g, which was approximately 2.0% the body mass of all tagged females. The hybrid tag had a profile above the back of the bird of 21 mm. For comparison, the Argos PTT tags fitted on sage-grouse have a profile of approximately 20 mm, which includes 5 mm of padding. We did not find evidence of scabbing or tissue on the harness of any of the hybrid tags we retrieved after mortality events.

Throughout the year, the GPS loggers maintained high voltage (mean voltage = 4.04 ± 0.10) when set to collect 6 GPS points/24-hour period. The voltage dropped very minimally (average voltage = 4.02 ± 0.11) when set to collect 48 locations/24-hour period, even through the winter when annual solar radiation is lowest. When ground-tracking sage-grouse, the average distance to download GPS data from the loggers was 148.29 ± 14.04 m (range = 8.57–718.57 m).

As of October 2018, the independent VHF allowed us to recover 32 missing tags that had power loss or damage due to a predation event, unknown mortality, or, possibly, slipped tags. The majority of these were found undamaged but with the solar panel facing the ground or obstructed by vegetation. Grouse remains or evidence of depredation were present at the locations where the majority (*n* = 25) of these tags were retrieved. We did not find evidence of mortality at locations for 7 retrieved tags; therefore, it is possible these were slipped tags.

3.4.1 Cost comparison

The overall costs for tags and data collection for a sample of 30 sage-grouse was highest for Argos PTT tags (US$125,372), followed by the hybrid tags (US$94,280), and VHF necklaces (US$60,620; Table 1). For the first comparison, with Argos PTT and hybrid tags standardized at 5 locations/day, the costs per datum for VHF necklaces (US$63.15) was 8 times greater than Argos PTT tags (US$7.46) and 11 times greater than hybrid tags (US$5.61). Costs per datum diverged more when hybrid tags were collecting 336 locations/week (every 30 min) versus Argos PTT tags collecting 105 locations/week (15/day) and VHF necklaces with 2 locations/week. At this collection frequency, cost per datum of Argos PTT tags (US$2.48) was 4 times more than hybrid tags (US$0.60) and costs per datum of VHF necklaces (US$63.15) was 105 times the cost of hybrid tags and 25 times the cost of Argos PTT tags.

3.5 Discussion

The extensive testing and history of biotelemetry use on sage-grouse provides valuable information applicable to other, less studied, species. We tested a unique combination of a solar GPS logger coupled with an independent VHF tag to maximize our return on investment. For our research, this return resulted in frequent and reliable location data and a robust sample of tagged individuals to better inform population-level inference and demography. Coupling a GPS logger with a VHF tag proved to be beneficial in several ways, some of which were not anticipated. The hybrid tag was ideal for weekly tracking in the field to collect demographic data while simultaneously collecting high-resolution temporal and spatial data. The VHF tag, with an independent battery, proved critical in retrieving tags after a mortality. Further, our cost comparison demonstrated that the hybrid tag was the most cost-effective option given our research objectives.

Technological advances have reduced the mass and size of tags, resulting in more opportunities to collect location data from smaller species and species that fly (Bridge et al. 2011). However, combining 2 technologies into one unit, while maintaining independent power sources, is often not feasible because of the mass of the combined units exceeds tag mass-to-body mass ratio recommendations. Researchers have added independent VHF to Argos PTT tags, primarily to aid in tag recovery (Bedrosian and Craighead 2010, Hansen et al. 2014). Hansen et al. (2014) experimented with 2 types of VHF add-ons with and combined unit mass of 35–40 g, which is ≥5 g heavier than our hybrid tags and >3% body mass of an average adult female sage-grouse (Connelly et al. 2003). However, tag mass limitations were less restrictive for their research because the tags were fitted on male sage-grouse with average mass >1,000 g more than females (Beck and Braun 1978). The low mass of the GPS logger (Harrier-L) we used permitted the addition of a VHF tag with a battery life expectancy of 2 years and a pulse rate adequate for efficient tracking while staying below the commonly recommended tag to bird ratio of ≤3% (Bridge et al. 2011).

As with Argos PTT tags fitted on sage-grouse, the GPS loggers we used are dependent on the solar panel receiving enough light to maintain battery power. As a result of mortalities and obstructed solar panels, Hansen et al. (2014) lost 7 Argos PTT tags (~US$28,000) during the first year of their sage-grouse study. Some of their Argos PTT tags were retrieved by extensively searching the last GPS location that was transmitted to the satellite; however, these 7 tags were not found at the last transmitted location. The VHF add-on allowed us to retrieve 32 hybrid tags the first 2 years of our study. Without the independent VHF, we would have lost approximately US$51,000 in transmitter costs in addition to the location data stored on these loggers. Unlike Argos PTT tags, we generally did not have a GPS location to focus our searching efforts because we were manually downloading data in the field, not receiving location data remotely (e.g., remote download from satellite relay). Therefore, if the GPS logger shut off because of a lack of power, we did not have a recent location to focus our searching efforts. We did not anticipate this many tags would have power loss due to obstructed solar panels; however, similar to Hansen et al. (2014), it was common after a predation event for us to find the tag upside down with the solar panel facing the ground. Also, depending on the amount of damage inflicted on the tag, most can be refurbished for a fraction of the cost of purchasing new tags.

Power-management is an important consideration when choosing a tracking technology. The amount of sun exposure a solar tag receives changes seasonally with shorter days and low light conditions in temperate and polar winters and can also be affected by a species' behavior. For example, when tagged sage-grouse were on nests, which were underneath vegetation, the solar panels received less light and voltage dropped (≤0.2 V). Wintering sage-grouse will snow-burrow during severe winter weather, which has the potential to reduce voltage over the short-term (Back et al. 1987). Researchers using Argos PTT tags on sage-grouse have set the tags to collect from 3 to 9 locations/day (Dzialak et al. 2011, Hansen et al. 2014, Smith et al. 2016, Pratt et al. 2017, Foster et al. 2018). Dzialak et al. (2011) increased their Argos PTT tags to collect 15 locations/day from 15 May to 15 July when the solar panels were receiving sufficient sunlight. Compared with satellite systems, our GPS loggers use much less power for data transmission because these data are transmitted over a much shorter distance (Bridge et al. 2011). With a sampling frequency of 6 locations/day, our GPS loggers maintained high voltage year-round. We saw a small decrease in average voltage (voltage ~0.02) when the hybrid tags were collecting 48 locations/day. When compared with Argos PTT tags, the GPS loggers–VHF tags were able to collect 3 times the amount of location data while maintaining adequate battery power. Based on our experience, we suspect we could increase the locational frequency while maintaining power above manufacturer recommended minimum voltage.

Both the Argos PTT tags and the Harrier-L GPS loggers provide options that allow for ground-tracking using a UHF or VHF signal with additional equipment. However, the ground-tracking option is powered by the same battery; therefore, is also dependent on the solar panel receiving adequate sunlight to maintain power. Further, the ground-tracking option requires additional power from the battery that reduces the power available for gathering GPS locations and transmitting locations to a satellite or a base station.

Prior to the development of GPS tracking systems, relocation data were often impossible to collect in large enough quantities or at fine enough resolutions to answer many research questions for free-ranging wildlife (Hebblewhite and Haydon 2010, Thomas et al. 2011, Kays et al. 2015). Satellite relay GPS technology (e.g., Argos) provides highly precise spatial and temporal location data to a degree never before possible with VHF tracking (Hebblewhite and Haydon 2010, Kays et al. 2015). However, Hebblewhite and Haydon (2010) caution that there are also disadvantages of choosing GPS tracking technology over traditional VHF when researching animal ecology. Primary disadvantages, they discuss, include increased costs per tag leading to small sample sizes and poor population-level inference (Hebblewhite and Haydon 2010). Solely relying on obtaining data remotely from a computer can result in missed information and divorces ecologist from a field-based understanding of animal ecology (Hebblewhite and Haydon 2010). By coupling these 2 technologies, we believe we alleviated these tradeoffs.

Researcher presence in the field remains a necessary component of studies that require observational data. Yet, researcher presence does have a greater effect on study species, compared with data from tagged individuals that is only collected remotely (Fair et al. 2010). We took several steps to minimize adverse effects on sage-grouse in our study. For example, with the hybrid tags, we only needed to get in close proximity of tagged sage-grouse to confirm reproductive state or gather data such as the presence of chicks. Otherwise, we were able to download data from a distance that was unlikely to disturb the tagged grouse and their flock mates.

We maintained reasonable sample sizes because of the cost savings associated with using a ground-based GPS logger (data retrieved by mobile base station instead of satellite; Thomas et al. 2011) instead of a satellite relay unit. The upfront costs of our hybrid tags were less than half the costs of Argos PTT tags. These cost savings allowed us to tag twice as many individuals (*n* ~ 40) as we would have using Argos PTT tags. When considering the net cost per datum of these different tracking technologies, we found that VHF necklaces were the most expensive choice, followed by Argos PTT tags and hybrid tags. When we assessed common GPS location collection frequencies associated with these different technologies used in sage-grouse research, we found that costs per datum for our hybrid tags was 25% less than Argos PTT tags. The cost per datum diverged more when we compared our highest GPS acquisition frequency (48 points/day) with the highest Argos PTT tag frequency we found in the literature (15 points/day). We wanted to provide a conservative comparison between Argos PTT tags and our hybrid tags; therefore, we assumed that no field visits would be required when using Argos PTT tags and that reproductive state would be determined based on location and movement data alone (Webb et al. 2012). However, if researchers using Argos PTT tags wanted to collect demographic data (e.g., brood survival) consistent with the data we collected using hybrid tags, a similar amount of field effort would likely be required. This, of course, would further increase the costs associated with Argos PTT tags and result in an even greater discrepancy between cost per datum.

The number of hybrid marked sage-grouse that went missing due to our inability to locate the VHF signal was relatively few during our study. However, we acknowledge the potential for large unexpected movements that would have resulted in an increase in the number of missing hybrid tags, which could impact cost comparisons for other research studies. Further, we recognize that VHF battery life, especially given the small size of VHF units used (i.e., ≤ 10 g), as it relates to study duration and objectives is an important issue when considering cost comparisons.

Cost per datum is a valuable way to compare different tracking technologies when high-frequency location data are required to meet research objectives (Thomas et al. 2011). However, if frequent location data are not necessary to meet the objectives of a study than cost per datum is not a valid comparison metric. For example, drawing from the sage-grouse literature, if the intent of the study is to assess how female survival rates are affected by anthropogenic features over a large landscape then a robust sample of VHF-tagged individuals is preferable to a much smaller sample fit with Argos PTT tags or hybrid tag

(Dinkins et al. 2014*a*). In this case, having an adequate sample of individuals to model survival outcomes is much more important to the objectives of the study than having frequent location data from fewer individuals. If one just looks at initial costs of the tracking technologies compared in this paper, 240 VHF necklaces could be purchased for the same price as 30 hybrid tags.

To achieve our research objectives, we regularly tracked hybrid-tagged sage-grouse in the field to verify reproductive state and gather demographic data (Kirol et al. 2015*a*, Smith et al. 2018). For instance, by ground-tracking sage-grouse weekly we were able to confirm the fate of sage-grouse nests (nest survival), confirm whether a female was brooding chicks or whether she was no longer with chicks (brood survival and reproductive state), and gather information on depredation events (causes of mortality). These data were not only important to our research objectives, but also helped us to better understand fitness outcomes associated with habitat selection, which are often overlooked in ecological research (Kays et al. 2015).

The hybrid tag we designed would be most beneficial for species of which tag mass is a limiting factor (i.e., smaller, volant species) and for species that do not undergo long-distance migrations. The hybrid tag would be less effective on a long-distance migratory species because of the effort and costs associated with using a VHF to track birds over large areas (Cochran 1987, Bridge et al. 2011). For long-distance migrants, either satellite-relay GPS (e.g., Argos) or a cellular-relay GPS (GPS data is transmitted through cellar networks) tags would likely be a more appropriate choice because GPS location data could be acquired while the bird was migrating and location data would not be lost if the bird died at an unknown location during migration or did not return to the area of original capture (Bridge et al. 2011). However, researchers studying migratory raptors with high site fidelity are using Harrier-L GPS loggers to collect location data when the species returns to a breeding territory by setting up stationary base stations in these territories (Blakey et al. 2020).

Sage-grouse typically move short distances within seasonal habitats (Fedy et al. 2012). In our study region, the longest movements recorded (~12 km) occurred when sage-grouse moved to wintering areas (Fedy et al. 2012). Consequently, our tag design would be best applied to research on largely resident or short-distance migratory populations and species. Many Galliformes are either nonmigratory or only make short-distance movements. Therefore, we believe the hybrid tag would be beneficial for research on many Galliformes, especially when observation data are needed in conjunction with high-resolution location data. A few examples include the lesser and greater prairie-chicken (*Tympanuchus pallidicinctus*, *T. cupido*) and Columbia sharp-tailed grouse (*T. phasianellus columbianus*), in North America; the black grouse (*Tetrao tetrix*), capercaillie (*Tetrao urogallus*), and red grouse (*Lagopus lagopus*) in Europe; and Reeves's pheasants (*Syrmaticus reevesii*) in Asia, all of which are relatively localized year-round (Johnsgard 1983, Giesen and Connelly 1993, Hagen and Giesen 2005, Xu et al. 2009, Johnson et al. 2011*a*).

Many new tracking technologies have become available to wildlife researchers over the past few decades, and each has strengths and weaknesses (Bridge et al. 2011, Thomas et al. 2011, Kays et al. 2015). In designing our hybrid tag and harness system, we hoped to reduce effects on sage-grouse, increase the amount and reliability of collected location data, maintain our ability to track birds in real-time from the ground, and decrease costs and increase sample size compared with satellite GPS transmitters. Our hybrid tags proved to be the most cost-effective option to meet the objectives of our study. Cost savings compared with satellite systems allowed us avoid sacrificing sample size while still gathering high-resolution location data. Hebblewhite and Haydon (2010) argue that emerging GPS-tracking technologies should not replace field biology but be used in conjunction to effectively research animal behavior and ecology. Our hybrid tags accomplish this by coupling traditional VHF tracking methods and field-based observational data with newer GPS tracking that provides accurate and more frequent location data.

Chapter 4

Does habitat reclamation following energy development benefit songbird nest survival?

4.1 Abstract

Songbird communities that rely on sagebrush habitat for breeding are experiencing steep population declines, while a large amount of the sagebrush ecosystem continues to be impacted by energy development. Reclamation is increasingly emphasized as a means of mitigating impacts on species that have been affected by oil and gas development; however, the response of sagebrush species to reclamation has largely been untested. We used nest survival of the Brewer's sparrow (*Spizella breweri breweri*), a sagebrush-obligate songbird of conservation concern, as an indicator of reproductive responses to early-stage reclamation in sagebrush habitat. Addressing the question: does early-stage reclamation provide a population benefit for the Brewer's sparrow? We assessed oil and gas reclamation ~5 years after reclamation, but sagebrush reestablishment is a slow process; thus, the legacy of these disturbances (i.e., disturbance scars) will likely remain for decades. We compared Brewer's sparrow nest survival across a gradient of oil and gas development from undisturbed and active development to areas that have undergone oil and gas reclamation. Nest survival was assessed at multiple scales from microhabitat to landscape. Additionally, our study was designed to help us better understand the mechanisms that affect songbird nest survival in oil and gas development fields such as the disturbance scare (e.g., the physical footprint of development) or infrastructure features. The distribution of nest sites in the active and reclamation areas suggested local avoidance of disturbance, both active disturbance and reclamation, when establishing nesting territories. We found that early-stage reclamation benefited nest survival at a local scale which suggests that infrastructure, and the associated human activity, may be more influential on Brewer's sparrow nest predation risk than the disturbance scar. Our findings demonstrated scale-dependent nest survival relationships. Across microhabitat and landscape scales, sagebrush canopy cover and composition are important to Brewer's sparrow reproductive success. Combined, these finding emphasize the importance of avoiding the removal of sagebrush habitat whenever possible and expediting sagebrush regeneration in disturbed areas to maintain high quality sagebrush habitat for breeding songbird populations.

4.2 Introduction

Sagebrush ecosystems in North America provide habitat for approximately 350 plant and animal species, many of which are species of conservation concern (Knick et al. 2003, Davies et al. 2011). A large amount of the sagebrush ecosystem has been – or has the potential to be – impacted by energy development, primarily in the form of oil and gas (Copeland et al. 2011, Allred et al. 2015). Songbirds that rely on sagebrush habitat for breeding are one of the bird communities in North America experiencing the steepest population declines (Sauer et al. 2013, Rosenberg et al. 2016). Sagebrush specialist songbirds including the Brewer's sparrow (*Spizella breweri breweri*) and sage thrasher (*Oreoscoptes montanus*) have declined by 35% and 44%, respectively, since 1970 (Rosenberg et al. 2016). During the same timeframe, grassland specialist songbirds that often use sagebrush habitat for nesting such as the vesper sparrow (*Pooecetes gramineus*) and lark bunting (*Calamospiza melanocorys*) have also declined by 30% and 86%, respectively (Rosenberg et al. 2016). When nests of these different species co-occur in sagebrush patches, they are exposed to similar environmental conditions and predation risks during the nesting period.

Energy development fields can be risky for songbirds because of direct mortalities and reduced fitness rates (Bayne and Dale 2011, Hethcoat and Chalfoun 2015*a*, Bernath-Plaisted and Koper 2016). Anthropogenic habitat modification can lead to maladaptive breeding strategies in birds in which behavioral cues become mismatched with survival and reproductive outcomes (Robertson and Hutto 2006). Nest productivity is a critical component of population persistence in birds (Saether and Bakke 2000) and increased predation is the primary mechanism that lowers nest survival in many habitats affected by anthropogenic development (DeGregorio et al. 2014, Hethcoat and Chalfoun 2015*a*, Bernath-Plaisted and Koper 2016). Anthropogenic habitat modification can result in heightened risk of nest predation due to changes in predator communities (e.g., expansion of novel predators that benefit from human subsidies), predator abundance, and predator-prey interactions (Winter et al. 2000, Chalfoun et al. 2002, Howe et al. 2014, Kirol et al. 2018). The specific mechanisms that drive impacts of energy development (i.e., increased predation risk) on songbird nest survival are not well understood. Impacts of energy development on songbird nest survival have been attributed to the physical footprint of development (native habitat removal, fragmentation and anthropogenic edge; Hethcoat and Chalfoun 2015*a*, Bernath-Plaisted and Koper 2016, Sanders and Chalfoun 2018) and to specific energy infrastructure features such as power lines (DeGregorio et al. 2014).

Habitat fragmentation describes reduced habitat patch size, greater distance between patches, and increases in novel, often non-native, vegetation types (Andrén 1994). Edges are the transition zones between vegetation types and increase with habitat fragmentation (Murcia 1995). Research has demonstrated that changes in ecological conditions near edges can directly affect birds (Murcia 1995, Bayne and Dale 2011). For example, natural vegetation removal, habitat fragmentation, and anthropogenic edge can depress nest survival by increasing exposure to nest predators (Winter et al. 2000, Vander Haegen 2007, Hethcoat and Chalfoun 2015*b*).

Infrastructure features can negatively influence nest survival by giving nest predators a competitive advantage (DeGregorio et al. 2014, Howe et al. 2014, Bernath-Plaisted and Koper 2016). For instance, infrastructure (e.g., oil and gas structures and power lines) that can increase the abundance of perching predators and mid-sized mammalian predators (Liebezeit et al. 2009, DeGregorio et al. 2014, Howe et al. 2014). DeGregorio et al. (2014) found that indigo bunting (*Passerina cyanea*) nest survival was strongly and negatively influenced by distance to power lines. They also found that two primary nest predator species (American crows [*Corvus brachyrhynchos*] and brown-headed cowbirds [*Molothrus ater*]) used power lines as perching structures and frequently preyed on songbird nests near the power lines.

Research has demonstrated the importance of considering multiple spatial scales when evaluating population fitness rates; habitat fragmentation may affect fitness rates through different mechanism at different spatial scales (Robinson et al. 1995, Chalfoun et al. 2002, Stephens et al. 2004, Llyod et al. 2005). At landscape scales, nest predation of forest-nesting songbirds increases as the forests become more fragmented (Robinson et al. 1995). At a local scale, Bernath-Plaisted and Koper (2016) found that grassland-nesting vesper sparrows had lower nest success when nest sites were within 1 km of oil and gas infrastructure and nest success rates continued to decrease as the proximity to infrastructure decreased.

Development of oil and gas reserves requires the clearing of vegetation for well pads and supporting infrastructure including access roads, facilities, and pipelines (sensu Walker et al. 2020). Oil and gas development is often considered a temporary disturbance because of the finite capacity of oil and gas production within areas and the mandated post-development reclamation that is generally required under conditions of approval by state and federal agencies (Andersen et al. 2009, Clement et al. 2014).

Reclamation generally refers to the rebuilding of soil profiles to reestablish plant communities (Pyke et al. 2015). Reclamation of oil and gas disturbances is associated with specific regulations which involve the removal of infrastructure, recontouring (reshaping the disturbed area to the original contour of the surrounding landform), preparation of topsoil surface and broadcasting of authorized native seed mixes over the reclaimed areas (U.S. Bureau of Land Management 2003, Rottler et al. 2018).

Post-development reclamation is increasingly emphasized as a means of mitigating declines of sagebrush associated species of conservation concern (U.S. Fish and Wildlife Service 2013, Clement et al. 2014). Reclamation is assumed to provide some immediate benefits to negatively impacted wildlife by removing potential population stressors, such as industrial noise, and above ground infrastructure. Much research has focused on the recovery of soil and vegetation following reclamation of disturbances in the sagebrush ecosystem (Avirmed et al. 2015, Davies et al. 2013, Gasch et al. 2016, Rottler et al. 2018). Yet, little research has looked at the response of sagebrush associated wildlife to reclamation following oil and gas disturbance (Barlow et al. 2020). To our knowledge no research has tested the effectiveness of reclamation as a mitigation measure. The recovery of plant communities in sagebrush ecosystems is particularly challenging because succession proceeds slowly in these arid habitats (Baker 2011, Rottler et al. 2018). Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), the dominant sagebrush species in our study area, can take more than 80 years to return to pre-disturbance size and structure (Baker 2011, Gasch et al. 2016, Avirmed et al. 2015, Rottler et al. 2018). Consequently, the legacy of oil and gas disturbance in sagebrush stands and the associated habitat fragmentation (contiguous areas of sagebrush broken into smaller, distinct and separate sagebrush patches) will also persist for decades after post-development reclamation takes place.

Brewer's sparrows are a short-lived sagebrush-obligate (i.e., dependent on sagebrush during critical life stages) songbird species that, under the right conditions, will attempt two and sometimes three nests per season (double and triple brood; Baker et al. 1976, Ehrlich et al. 1988, Rotenberry et al. 1999, Rowland et al. 2006). The sagebrush dependence during breeding and high potential reproductive output of the Brewer's sparrow makes them an ideal indicator species to assess the potential mitigating effects of reclamation on bird populations breeding in sagebrush habitat (Niemi and McDonald 2004).

In this study, we assess early-stage reclamation in sagebrush landscapes approximately 5 years after oil and gas infrastructure was removed. Reclamation areas in our study were revegetated with reclamation seed mixes but did not contain the sagebrush overstory component. Consequently, the vegetation structural characteristics of reclaimed areas in our study were similar to active oil and gas disturbances in that they both no longer contained the sagebrush overstory component. The primary difference between reclaimed areas and active disturbances was that reclamation no longer had the infrastructure features and, instead of graveled roads or hard surface well pads, had seeded grass and forb ground cover.

Therefore, comparing active oil and gas and reclamation soon after it took place provided a unique opportunity to better understand the mechanisms that affect songbird nest survival in oil and gas development areas. If, for example, infrastructure features or industrial noise are the primary drivers of increased nest predation in active oil and gas areas, we would expect nest survival rates to respond quickly and positively to reclamation. Conversely, if the primary causes of increased nest predation were driven more by increased edge and fragmentation, we would expect that oil and gas reclamation would not immediately benefit nest survival because of the legacy of the disturbance due to the slow reestablishment of the sagebrush overstory component.

We designed this study to address this question: how effective early-stage reclamation is at removing or minimize reproductive stressors (e.g., increased nest predation) that act on sagebrush breeding songbirds during oil and gas development and production? We explored this question across multiple spatial scales from landscape to microhabitat. We used nest survival of the Brewer's sparrow as an indicator of potential reproductive responses of sagebrush nesting birds to oil and gas reclamation treatments. At the landscape scale, we hypothesized that nest survival rates would be the highest within undisturbed (i.e., control) sites and the lowest within our active oil and gas sites. Because of the legacy of fragmentation and edge that remained in the reclamation areas, we expected that nest survival would also be lower in reclamation sites compared to undisturbed sites.

At local scales, we hypothesized that nests exposed to greater amounts of oil and gas disturbance and those in closer proximity to oil and gas infrastructure would have the lowest nest survival rates when compared to nests farther from the disturbance footprint. Furthermore, in the reclamation areas, we hypothesized that edge and fragmentation factors may continue to act to reduce nest survival of nests located in closer proximity to reclaimed areas. At the microhabitat scale, we hypothesized that sagebrush structure and cover immediately surrounding a nest would be predictive of nest survival and nests surrounded by less sagebrush cover, such as those immediately adjacent to reclamation or active edge, would have lower nest survival. Addressing these hypotheses will help us better understand the mechanisms that act to depress songbird nest survival in oil and gas development fields.

4.3 Methods

4.3.1 Study area

Our study area was located in sagebrush-steppe habitat in northeastern Wyoming, USA, within the Powder River Basin (PRB) region (44.2603ºN, -106.3095Wº; Figure 4.1). Dominant shrubs included big sagebrush, black greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* and *Ericameria* spp.). Common grasses included native species such as blue grama (*Bouteloua gracilis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and invasive species such as Japanese brome (*Bromus japonicas*) and cheatgrass (*B. tectorum*). In addition to the Brewer's sparrow, other bird species we documented nesting in sagebrush stands in our study area included: Brewer's blackbird (*Euphagus cyanocephalus*), greater sage-grouse (*Centrocercus urophasianus*), lark bunting, lark sparrow (*Chondestes grammacus*), loggerhead shrike (*Lanius ludovicianus*), mourning dove (*Zenaida macroura*), sage thrasher, spotted towhee (*Pipilo maculatus*), vesper sparrow and western meadowlark (*Sturnella neglecta*). Land use in the region was mainly oil and gas production and cattle ranching. Elevation ranged between 1268 m – 1442 m. Detailed descriptions of the region are available in previous publications that focused on the greater sage-grouse (e.g., Doherty et al. 2010, Fedy et al. 2015).

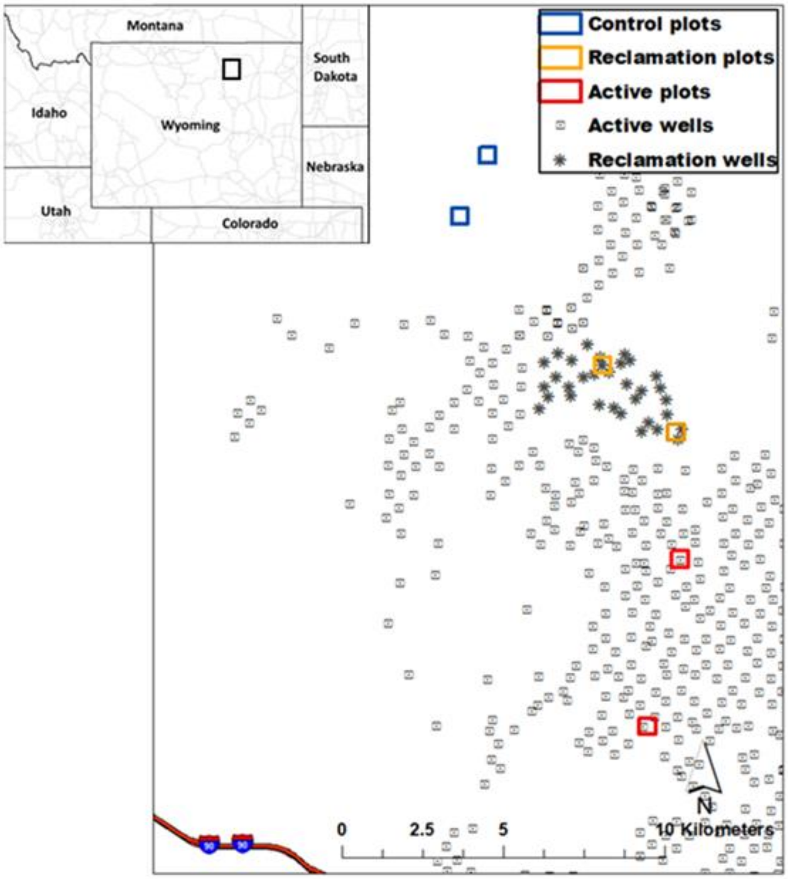


Figure 4.1: Map of study area and nest-searching plots for Brewer's sparrow in northeastern Wyoming, USA, 2016-2018.

4.3.2 Songbird indicator species

Brewer's sparrows begin arriving on their breeding grounds in late-April and depart by October (Walker 2004, Harrison and Green 2010). Brewer's sparrows defend territories and maintain spacing between nests (Rotenberry et al. 1999). In some areas, Brewer's sparrows have been shown to cluster their nesting territories in loose aggregations (Rotenberry et al. 1999, Harrison and Green 2010). Brewer's sparrows are thought to be monogamous (Hansley and Beauvais 2004). Males establish breeding territories and pairs are formed when the females arrive a few weeks later (Walker 2004, Harrison and Green 2010). The size of Brewer's sparrows breeding territories vary between regions, sites and years (Rotenberry et al. 1999). Reported territory sizes range between 0.25 - 2.0 hectares (Rotenberry et al. 1999, Walker 2004, Hansley and Beauvais 2004, Harrison et al. 2009). Brewer's sparrows build a small open-cup nest (~8cm diameter) with 3 to 6 eggs per clutch and will, generally, initiate two or three nests per season (Ehrlich et al. 1988, Rotenberry et al. 1999, Mahony et al. 2001). However, following nest failures, Brewer's sparrows have been observed nesting more than three times per season (Chalfoun and Martin 2007). Egg-laying to fledging takes about 20-22 days (Rotenberry et al. 1999, Hansley and Beauvais 2004).

4.3.3 Nest monitoring

We searched for Brewer's sparrow nests in six 500 x 500 m (0.25 km^2) plots distributed across the study area from 2016-2018 (Figure 4.1). Nest searching took place between early May and mid-July each season. We used auditory and visual clues to locate nests and recorded the location of all active nests. Most nests were found during egg laying and incubation periods. We monitored nests every second day and increased monitoring to every day as fledging approached (Martin and Geupel 1993). We used nestling morphology to determine hatching date (Martin and Geupel 1993, Jongsomjit et al. 2007) and nest age, if we found the nest during the nestling period (Nur et al. 2004, Jongsomjit et al. 2007). Nests were considered depredated if eggs or young chicks were absent from the nest or if there were other signs of predation such as damaged nest, fledgling remains or egg fragments. If a nest was close to the estimated fledging date and we did not identify any sign of fledging (e.g., feces, fledglings in area) we considered the nest depredated (Martin and Geupel 1993). Successful nests produced at least one Brewer's sparrow fledgling. If we believed a nest had fledged, we verified fledging by locating fledglings, observing adults carrying food or by listening for adult and fledgling communication calls close to the nest.

We calculated the nest initiation date (i.e., date the first egg was laid) on the basis of date of discovery of the nest and estimated age of the nest at discovery (Shaffer 2004). When the exact fate date (success or failed nest) was not known we assigned the nest fate date as the midpoint between the last monitoring intervals (Nur et al. 2004). Hatched nests, nests that survived the entire period, and nests with unknown fates, were right-censored (Hosmer and Lemeshow 2008). The exposure period (t) for our nest survival analysis was $t = 22$ days (egg laying = 3 days, incubation = 10 days, nestling stage = 9 days; Petersen et al. 1986, Rotenberry et al. 1999).

4.3.4 Treatment and control plots

Nest plots were selected across a gradient of energy development that included three categories: 1) reclaimed oil and gas, 2) active oil and gas, and 3) non-developed habitat. We refer to the active oil and gas and the reclaimed oil and gas as “treatments” and the non-developed habitat as the “control”. Our study area contained coal-bed natural gas (CBNG) wells that were developed at 3.1 well pads per km^2 (80-acre spacing; Kirol et al. 2015*b*). On average, CBNG well pads required the clearing of 0.5 ha of natural vegetation. Two nest searching plots were positioned in each treatment and control area. All nest plots were in sited in areas dominated by sagebrush landcover and were separated by >2 km to ensure independence (Figure 4.1).

4.3.4.1 Reclamation and active disturbances

Active disturbances are surfaces that have been stripped of natural vegetation and are associated with producing CBNG wells (i.e., active wells), graveled access roads and other supporting infrastructure (Figure 4.2). We refer to previously active disturbances (e.g., wells and access roads) that have been reclaimed as reclamation or reclamation surfaces (Figure 4.2). Reclamation surfaces have undergone reclamation that included the removal of all infrastructure, stripping and re-spreading topsoil, and re-contouring well pads, access roads and other infrastructure disturbances (U.S. Bureau of Land Management 2003). Once these reclamation surfaces were prepared, seeding was completed with a no-till drill (U.S. Bureau of Land Management 2003). The reclamation site in our study contained 30 CBNG wells that were plugged and reclaimed in 2013 (Figures A1 and A2). The area influenced directly by reclamation of these 30 CBNG wells was ~8.6 km^2.

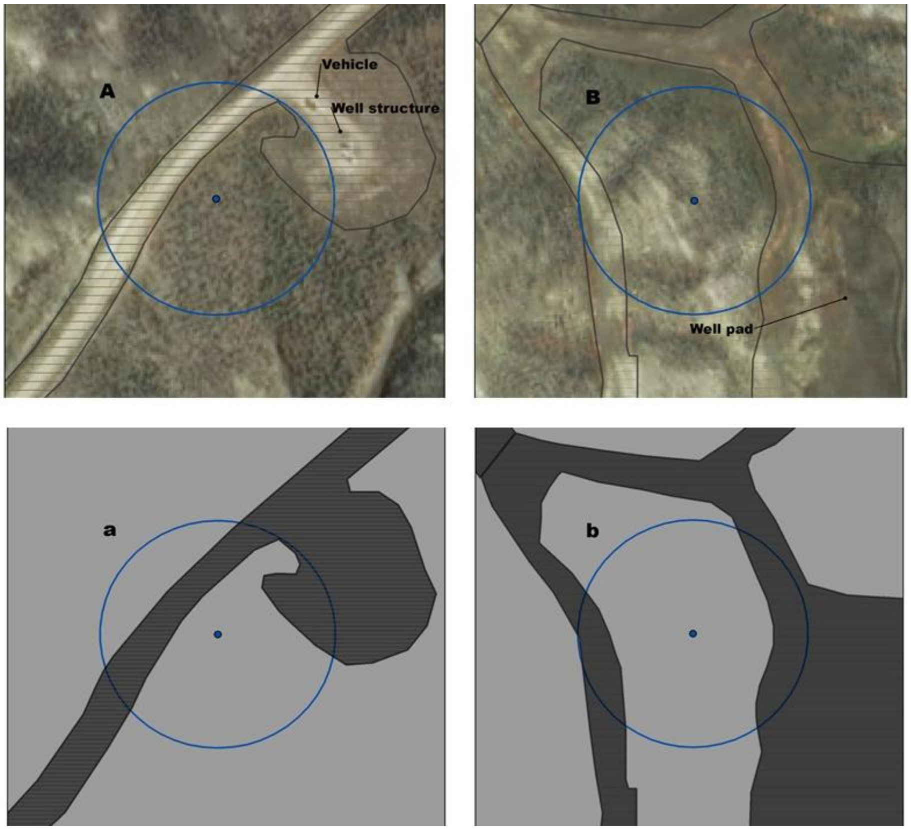


Figure 4.2: The physical footprint of disturbance quantified using heads-up digitizing and converted to a 1-m raster for analysis. Selected Brewer's sparrow nests (blue dots) and 50m radius scale (blue circles), northeastern Wyoming, USA. Panel A shows the area digitized as active disturbance and panel B shows area digitized as reclamation with imagery in the background. The disturbance polygons encompassed all of the area disturbed (e.g., sagebrush removed) for the well pads and access roads (panels a, b). Some of the disturbed habitat around active development (A) had filled in with grass and forb cover. The reclaimed surface was dominated by grass and forb cover and did not contain sagebrush (B). Nests were exposed to 25% active disturbance (panels A, a) and 23% reclamation (Panels B, b) within 50m.

4.3.5 Nest plot selection

We selected control, active and reclamation nest plots that contained similar vegetation types, such as being dominated by sagebrush landcover, to minimize influences of natural variation (e.g., elevation, topography and vegetation community) and maximize the isolation of the treatment effects of interest (i.e., active oil and gas and reclaimed oil and gas disturbances). Because the reclamation site was the most spatially limited treatment, we first selected plots within this treatment and used the habitat characteristics of the reclamation treatment plots to guide the selection of the active treatment and control plots. Using geographic information systems (GIS), we first selected reclamation plots based on four primary criteria: 1) sagebrush was the dominant landcover, 2) contained at least one reclaimed CBNG well, 3) ≥600m from an active natural gas wells, ≥300 m from gravel access roads and overhead power lines, and 4) located predominantly on public land (Wyoming State or BLM). These influence distances for wells, roads and power lines were informed by previous research on the response of songbirds to development (Ingelfinger and Anderson 2004, Bayne and Dale 2011, Yoo 2014, Thompson et al. 2015).

We then used spatial layers representing elevation, and vegetation cover in GIS to match active and control treatment plots to the range of vegetation and topographic characteristics of the reclamation plots. Based on the values derived from the reclamation plots, the active treatment and control plots we selected had average sagebrush cover of 10-14%, terrain roughness values between 50-550, and an average elevation between 1,200-1,400 m. Additionally, the active treatment plots contained ≥1 well(s) to provide a direct comparison to the reclamation plots that contained ≥1 well(s) that had been reclaimed. This GIS assessment provided a candidate set of control and active plots that were randomly numbered. We then sequentially went through these plots and selected the first plots that we confirmed met all of these criteria and that were accessible for field work. Sagebrush spatial layers for site selection were processed from Wyoming sagebrush products (Homer et al. 2012). Roughness values were based upon a terrain roughness index (Evans et al. 2014), derived from a Digital Elevation Map (DEM). Average elevations within plots were also calculated from a DEM (Evans et al. 2014). All plots were separated from each other by >1 km.

4.3.6 Microhabitat covariates

In most bird species, nest predation is the foremost cause of nest failure; consequently, birds select habitats to hinder detection by potential predators (Ricklefs 1969, Martin 1993). Microhabitat characteristics can influence nest survival of sagebrush associated birds (Coates and Delehanty 2010, Ruehmann et al. 2011). We measured and compiled a suite of biologically-relevant microhabitat covariates at nest locations (Table 4.1). At microhabitat scales, research has demonstrated that vegetation components contributing to greater vertical and horizontal nest concealment of ground and shrub-nesting birds often has a positive relationship with nest survival in real and experimental nests (Martin 1998, Harrison and Green 2010, Latif et al. 2012, Maresh Nelson et al. 2018). Covariates directly related to nest concealment assessed in our nest survival models included: total visual obstruction (VisualObst), nest shrub vigor (Vigor), grass height (GrassHeight), percent sagebrush cover (PercARTRL), sagebrush plant density (DenseARTRL), average sagebrush height (HeightMean) and variability in sagebrush height (HeightSD). Greater proportions of bare ground (BareSoil) surrounding a nest site can influence nest survival in passerines in both positive and negative directions (Martin 1998). Latif et al. (2012) found that experimental yellow warbler (*Dendroica petechia*) nests that were higher above the ground (e.g., positioned higher in the shrub or in a taller nest shrub) experienced higher avian predation rates. Covariates related to nest height assessed in our nest survival analysis were nest shrub height (ShrubHeight) and height from ground to the nest (NestHeight). Greater grass and forb cover can be positively associated with the abundance of deer mice (*Peromyscus maniculatus*), which are known to depredate Brewer's sparrow nests (Hanser et al. 2011, Heathcoat and Chalfoun 2015*a*, Sanders and Chalfoun 2018). Additionally, the establishment of nonnative grasses can alter Brewer's sparrow nest predation risk. Ruehmann et al. (2011) found that Brewer's sparrow nesting in areas with an understory dominated by smooth broom (*B. inermis*), an exotic grass, had higher nest survival than those nesting in areas with a native understory. They propose that this nonnative grass may have provided greater nest concealment (Ruehmann et al. 2011). In our nest survival models, we assessed a native grass cover covariate (Grass) and a nonnative grass cover covariate (InvasiveGrass) as well as a forb cover covariate (Forbs).

Table 4.1: Covariates assessed in Brewer's sparrow nest survival models representing multiple scales from the individual nest shrub to a 100m radius around a nest, Wyoming, USA.

Covariate	**Scale**	**Description**
Microhabitat		
ShrubHeight	Nest shrub	Height of shrub, excluding inflorescences (cm)
NestHeight	Nest shrub	Height to the bottom of nest cup from ground (cm)
Vigor	Nest shrub	% of alive foliage (nearest 10%)
Grass	5m radius	% grass cover, excluding invasive grass
InvasiveGrass	5m radius	% invasive grass cover (*Bromus tectorum* and *B. japonicas*)
Forbs	5m radius	% forb cover
BareSoil	5m radius	% bare ground cover
GrassHeight	5m radius	Average grass droop height (cm), excluding invasive grass
VisualObst	5m radius	Visual obstruction (horizontal cover; dm)
PercARTRL	5m radius	% live big sagebrush (*Artemisia tridentata*) canopy cover
DenseARTRL	5m radius	Average live big sagebrush density (plants/m^2)
HeightMean	5m radius	Average big sagebrush height (cm)
HeightSD	5m radius	Variability (standard deviation [SD]) in sagebrush height
Spatial		
NDVI	30, 50, 100 (m) radii	Mean NDVI (Normalized Difference Vegetation Index) value per scale (30-m resolution; Robinson et al. 2017)
ForbGrs	30, 50, 100 (m) radii	Mean forb and grass understory cover per scale (30-m resolution; Jones et al. 2018)
BigSage	30, 50, 100 (m) radii	% big sagebrush cover per scale (30-m resolution; Xian et al. 2015)
SageHgt	30, 50, 100 (m) radii	Average big sagebrush height per scale (30-m resolution; Xian et al. 2015)
SDSageHgt	30, 50, 100 (m) radii	Variability (SD) in sagebrush height per scale (30-m resolution; Xian et al. 2015)
Anthropogenic		
ActiveDist	30, 50, 100 (m) radii	% active disturbance footprint per scale (1-m resolution)
RDist	30, 50, 100 (m) radii	% reclamation footprint per scale (1-m resolution)
PwrLine	30, 50, 100 (m) radii	Distance to nearest overhead power line as a decay per scale

Temporal		
Year	NA	Study year
JulianDay	NA	Julian date of start of nest incubation

4.3.7 Microhabitat sampling

We sampled microhabitat characteristics of the nest shrub and the immediate area surrounding the nest shrub (i.e., nest patch). The nest shrub formed the center of two perpendicular 10m transects. We measured vegetation characteristics such as shrub canopy cover, shrub density, shrub heights, ground vegetation cover and visual obstruction. Barlow et al. (2019) provides a detailed description of our microhabitat sampling methods (Table 4.1). To minimize detrimental effects on nest initiation and egg and chick survival, we sampled Brewer's sparrow nest sites after the Brewer's sparrow nesting season concluded each year.

4.3.8 Spatial covariates

In addition to our microhabitat data collected in the field, we also quantified habitat structure by summarizing GIS data across three larger spatial scales because songbird nest survival can be influenced at multiple spatial scales (Stephens et al. 2004). The spatial scales we assessed were informed by previous research on Brewer sparrows (Rotenberry et al. 1999, Carlisle et al. 2018*a*). The radii of these three scales were 30m, 50m and 100m. Within these scales we used zonal statistics to calculate vegetation covariates including mean Normalized Difference Vegetation Index (NDVI), mean forb and grass understory cover, percent big sagebrush canopy cover, average sagebrush height (cm) and the standard deviation of sagebrush height (Table 4.1; Xian et al. 2015, Robinson et al. 2017, Jones et al. 2018, Yang et al. 2018). NDVI is as a measure of primary productivity (Robinson et al. 2017). The standard deviation in sagebrush height represented sagebrush height variability. Higher standard deviation values were associated with greater horizontal heterogeneity and lower values with lower horizontal heterogeneity in sagebrush plants (sensu Williams et al. 2011).

In addition to grass and forb cover, NDVI has been shown to be predictive of deer mice abundance (Hanser et al. 2011). Greater deer mice abundance negatively affects Brewer' sparrow nest survival (Heathcoat and Chalfoun 2015*a*, Sanders and Chalfoun 2018). We used dynamic 30-m resolution NDVI products generated every 16 days (Robinson et al. 2017) to calculate Mean NDVI layers. We obtained four NDVI composites from approximately May 9th to June 26th to overlap the Brewer's sparrow nesting period each year (2016 – 2018). We then averaged these four composites to generate NDVI values to match with those year's nests. We used available 30-m resolution annual forb and grass and perennial forb and grass percent cover layers for each year of the study (Jones et al. 2018). We summed the annual and perennial forb and grass layers to generate a forb and grass percent cover value per scale (Table 4.1). We used 2016 shrubland layers (30-m resolution) available through the U.S. National Land Cover Database (NLCD) to calculate vegetation concealment covariates including percent big sagebrush canopy cover, average sagebrush height (cm) and the standard deviation of sagebrush height per scale (Xian et al. 2015, Yang et al. 2018).

Predation is the most important process affecting nest survival of songbirds and anthropogenic modifications of nesting habitat can increase nest predation risk (Vander Hagen 2007, Heathcoat and Chalfoun 2015*a*, Bernath-Plaisted and Koper 2016). We quantified disturbances at each scale that were associated with active oil and gas (e.g., wells) or reclamation (e.g., reclaimed roads) surfaces. We used National Agriculture Imagery Program (NAIP) imagery to heads-up digitize the physical footprint of disturbance at a 1:1000 screen resolution and converted these disturbance polygons to a 1-m resolution raster layer (http://datagateway.nrcs.usda.gov). We quantified active disturbance and reclamation as the percent area per scale (Figure 4.2). All GIS data was processed using ArcGIS Desktop 10.7 (http://www.esri.com) and QGIS 3.10 (qgis.osgeo.org).

Overhead power lines are a type of supporting infrastructure that is generally not associated with a physical footprint or removal of habitat. In oil and gas development areas, including our study area, power lines often span undisturbed sagebrush habitat with minimal surface disturbance (i.e., a power pole approximately every 100m). Proximity to power lines can negatively influence songbird nest survival because some avian nest predators use power lines and poles as perching structures (DeGregorio et al. 2014). We quantified distance from nests to power line using exponential distance decay functions to account for decreasing magnitude of influence with an increasing distance from the power line on nest survival (Fedy and Martin 2011). Decay values were calculated using the form $e^{(-d/\alpha)}$ where d was the distance in meters (from nest to power line) and α was set to correspond to each radii – 30m, 50m and 100m (Table 4.1; Kirol et al. 2015*b*).

4.3.9 Modeling approach

To assess relationships between covariates and Brewer's sparrow nest survival we used a mixed-effects Cox proportional hazards model (function: *coxme*) in R (R version 3.6.0; Therneau 2020). We modeled environmental covariates that potentially influenced Brewer's sparrow nest survival from four categories that included temporal, microhabitat, spatial and anthropogenic disturbance. Temporal covariates included year and Julian date. We modeled year to account for potential variability in nest survival between years and Julian date because nest survival may be related to when the nest was initiated (Dinsmore et al. 2002). We selected models in three steps using sample-size-adjusted Akaike's Information Criteria (AIC_c), to compare and rank models within each step (Burnham and Anderson 2002) as described below. We standardized all covariates prior to modeling. We considered both linear and quadratic terms for the physical footprint of disturbance covariates because avian fitness metrics can have nonlinear relationships with exposure to increasing amounts of surface disturbance (Kirol et al. 2015*a*). We tested for potential correlation between covariates using Pearson's correlation matrix, we did not include any two co-varying variables ($|r| \geq 0.6$) in any model. When covariates were correlated, we selected the covariate with the lowest AIC_c in a single covariate model comparison. The single covariate model also contained the random effects plot and treatment described below. At each stage, the best-fit AIC_c model, that only contained informative parameters (Arnold 2010), was brought forward to the next model selection step. We disregarded models differing from the best-fit model by one parameter and within 2 $\Delta\mathrm{AIC}_c$ if the slope coefficient was uninformative with 85% confidence limits overlapping zero (Burnham and Anderson 2002, Arnold 2010).

To account for the spatial clustering of our nest data and allow us to share information across the sample of nests (Bolker et al. 2009, Kéry and Royle. 2016), our first step involved developing a model with plot identification and treatment type as categorical covariates (Figure 4.1). Plot was included as a random effect within treatment (nested structure) because our data were obtained from different nest plots ($n = 6$) within treatment areas ($n = 3$). This random-effect model structure was included in all subsequent modeling steps. For spatial covariates measured at multiple spatial scales, we first optimized the scale by comparing single covariate models, in combination with our random effects, and brought forward the covariate scale with the lowest AIC_c to the next modeling step.

In the second modeling step, we modeled the temporal covariates Julian date and year with our random effects to determine if these covariates improved model fit (Table 4.1). This model moved forward to the third modeling step, in which we considered microhabitat and spatial covariates. The best-fit model from this step, with the lowest AIC$_c$ and only containing informative parameters, formed our base-model (Webb et al. 2012, Kirol et al. 2015*b*). The purpose of the base-model was to account for environmental variation in Brewer's sparrow nest survival (i.e., as statistical control covariates; Hosmer and Lemeshow 2008) to facilitate interpretation of the anthropogenic covariates.

In our final modeling step, we tested decay distance to power lines and different functional relationships (linear and quadratic) of our surface disturbance covariates, at each scale, with our base-model. We assessed support for decay distance to power lines and different functional forms (i.e., linear or quadratic) of the disturbance covariates based on AIC$_c$ and the coverage of the 85% confidence intervals. If an anthropogenic covariate was influencing Brewer's sparrow nest survival, we expected the anthropogenic covariate would be informative, have 85% confidence interval coverage that did not overlap 0, when combined with the base-model (Arnold 2010, Bernath-Plaisted and Koper 2016).

We reported 85% confidence intervals for parameters to be consistent with the AIC$_c$ model selection process (Arnold 2010). For interpretation of the effect of a unit change in individual covariates on Brewer's sparrow nest survival, we modeled the non-standardized form of the supported covariates. To ensure that the proportional hazards assumption was not violated, we plotted Schoenfeld residuals for our final model as well as each individual covariate in our final model (Hosmer and Lemeshow 2008). For the purpose of reporting nest survival estimates for each treatment type and year we modeled them as fixed effects in univariate models (function: *coxph*; Therneau 2019).

4.4 Results

Our survival analysis included 107 Brewer's sparrow nests monitored between 2016-2018 ($n = 31$ in 2016, $n = 41$ in 2017 and $n = 35$ in 2018). Nest predation was the cause of nest failure in all of the nests included in our analysis. We did not identify a single nest that was located within the active disturbance or reclamation footprint. Model adjusted nest survival estimates for a 22 day Brewer's sparrow nest survival period for the entire sample were 54% (85% CI: 48–62%). Model adjusted Brewer's sparrow nest survival did not differ significantly ($P \geq 0.714$) between years (2016 = 56% [85% CI: 45–71%], 2017 = 53% [85% CI: 43–65%], 2018 = 54% [85% CI: 44–67%]) or differ significantly ($P \geq 0.257$) between active treatment (61% [85% CI: 51–72%]), reclamation treatment (51% [85% CI: 41–63%]) and control (47% [85% CI: 34–65%]).

4.4.1 Base model

Our best-fit model that formed our base-model contained temporal, microhabitat and spatial covariates: JulianDay, NestHeight (nest shrub), DenseARTRL (5m radius), and BigSage (100m radius). The predictive microhabitat covariates were live big sagebrush plant density (DenseARTRL; plants/m^2) and the height from the ground to the bottom of the nest cup (NestHeight). BigSage represents the percent of big sagebrush cover surrounding a nest. JulianDay, DenseARTRL, NestHeight and BigSage had 85% CIs that slightly overlapped 0 when combined with the other covariates in the best-fit model. We decided to retain these because they were present in the majority of the 2 ΔAIC_c model set and did not have overlapping 85% CIs unless all 4 of these covariates were in the same model (Table 4.2). BigSage and DenseARTRL were both positively associated with Brewer's sparrow nest survival. Our base-model predicts that as the amount of big sagebrush cover within 100 m of a nest and as the density of live big sagebrush shrubs within 5m of a nest increase the likelihood of that nest surviving also increases. Julian date (JulianDay) suggests that nests initiated later in the season are at greater risk of failure. Nest height suggests that nests built higher in the nest shrub experience higher risk than those built lower in the nest shrub (Table 4.2). When compared to the null model, the base-model (i.e., covariate adjusted model) explained much of the variability in nest survival between the active treatment (59% [85% CI: 49–71%]) and reclamation treatment (56% [85% CI: 46–69%]), but little variability between the two treatments and control (45% [85% CI: 32–64%]).

Table 4.2: Final Cox proportional hazard model describing relationships between temporal, microhabitat, spatial and anthropogenic covariates and Brewer's sparrow nest survival. The base-model accounted for environmental variation in Brewer's sparrow nest survival to allow for interpretation of the influence of anthropogenic disturbance covariates on Brewer's sparrow nest survival, Wyoming, USA.

			Risk ratio 85% CI	
Covariate (scale)	Coefficient	Risk ratio	Lower	Upper
Base-model with plot nested in treatment as a random effect				
JulianDay	0.224	1.251	1.015	1.543
NestHeight (nest shrub)	0.170	1.185	0.972	1.445
DenseARTRL (5m radius)	-0.248	0.781	0.626	0.973
BigSage (100m radius)	-0.156	0.856	0.673	1.088
Base-model + % active disturbance				
ActiveDist +	-0.523	0.592	0.346	1.013
ActiveDist^2 (50m radius)	0.642	1.901	1.127	3.210

4.4.2 Anthropogenic covariates

When combined with our base-model, decay distance to power lines (PwrLine) was not supported as having a relationship with nest survival at any of the scales assessed. We did not find support for a linear relationship between the amount of active disturbance (ActiveDist) and nest survival at any scale. At the 50m scale, the quadratic form of active disturbance (ActiveDist + ActiveDist^2) had the most support as having a relationship to Brewer's sparrow nest survival (Figure 4.3 and Table 4.2). The 85% CIs of the squared term did not overlap 0. But the linear term had 85% CIs that slightly overlapped 0 (Table 4.2). The quadratic form suggests that exposure of Brewer's sparrow nests to active disturbance within 50m initially did not influence nest risk until disturbance reached ~15%. Nest survival risk increased steeply when disturbance reached ~30% (Figure 4.3). At the 50m scale, 20% of our nest sample in the active treatment were exposed to ≥15% disturbance. The low sample size at the high end of the distribution (≥15%) increased uncertainty as demonstrated by the widening CIs (Figure 4.3). Our nest survival model predicted that the probability of a nest being successful is approximately 16% higher for nests not exposed to active disturbance compared to nests exposed to 30% active disturbance within 50m.

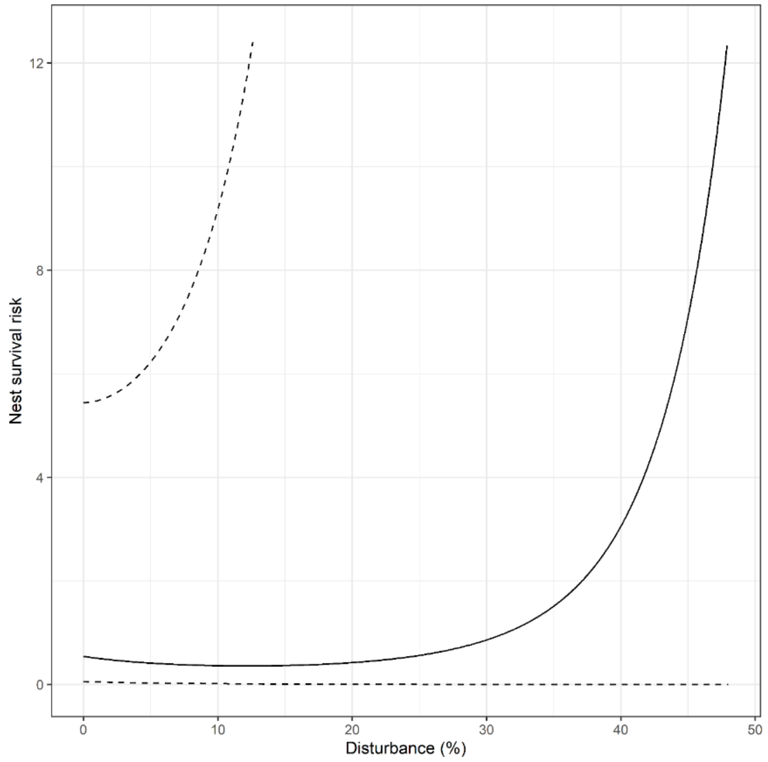


Figure 4.3: Brewer's sparrow nest survival risk and the percent active disturbance exposure at a 50m radius scale, northeastern Wyoming, USA. Dashed lines represent 85% confidence intervals.

Sixty-six percent of the active treatment nests were exposed to 0% disturbance at the 30m scale. At the 50m and 100m scales, 48% and 25% of the nests were exposed to 0% disturbance. The mean distance (± SE) from nests to the nearest active disturbance was 62.87 ± 7.12 m (range = 3.16–181.73 m). Across the two active nest-searching plots an average of 7.59 ± 0.80% (range = 6.79–8.40%) of the plot contained active disturbance. This amount of disturbance introduced an average of 2.38± 0.34 km (range = 2.04–2.72 km) of edge.

We did not find support for a linear or quadratic relationship between reclamation (ReclDist) and nest survival at the 50m scale or the other scales (30m and 100m radii) assessed. Exposure to reclamation is similar to that of active disturbance with 17% of the sample of nests in the reclamation treatment being exposed to ≥15% disturbance. To further examine potential differences in Brewer's sparrow nest survival when exposed to reclamation instead of active disturbance, we modeled the quadratic term at the same scale (50m radius) as the supported active disturbance relationship and found that in addition to the lack of statistical support the coefficient slope is relatively flat (Figure 4.4).

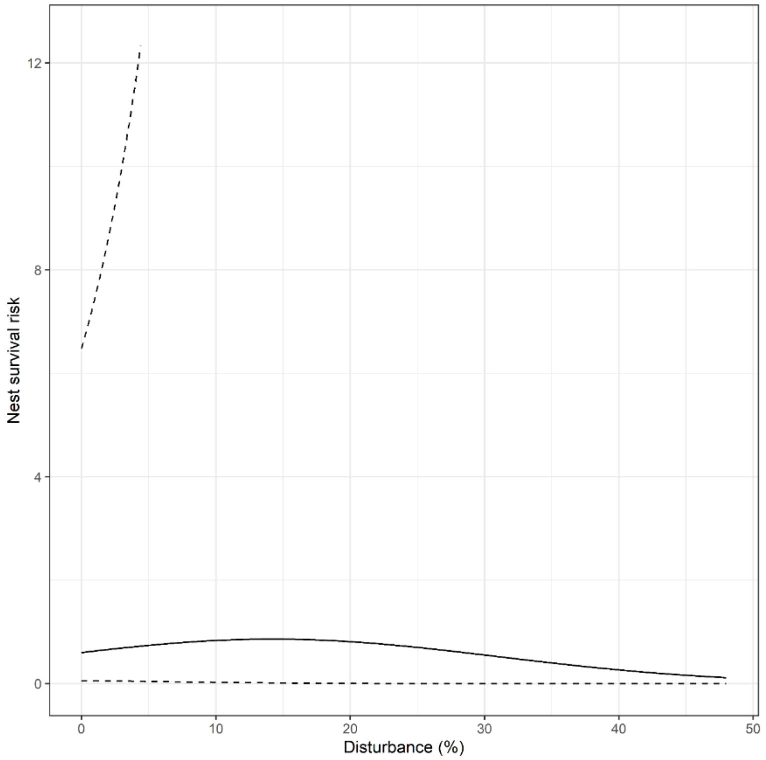


Figure 4.4: Brewer’s sparrow nest survival risk and the percent reclamation exposure at a 50m radius scale, northeastern Wyoming, USA. Dashed lines represent 85% confidence intervals.

Of the reclamation treatment nests, 78% were exposed to 0% disturbance at the 30m scale, 46% were exposed to 0% disturbance at the 50m scale and 23% were exposed to 0% disturbance at the 100m scale. The mean distance from nests to the nearest reclamation surface was nearly equivalent to the active treatment nests (61.41 ± 6.47 m [range = 3.00–161.28 m]). Across the two reclamation nest-searching plots an average of 9.47 ± 2.31% (range = 7.17–11.78%) of the plot contained reclamation. This amount of reclamation surface introduced an average of 2.26 ± 0.27 km (range = 1.98–2.53) of edge.

Our final model explaining Brewer’s sparrow nest survival included multiple scales from the individual nest shrub to the amount of big sagebrush cover in a 3.14 hectare (100 m radius) area around a nest (Figure 4.5).

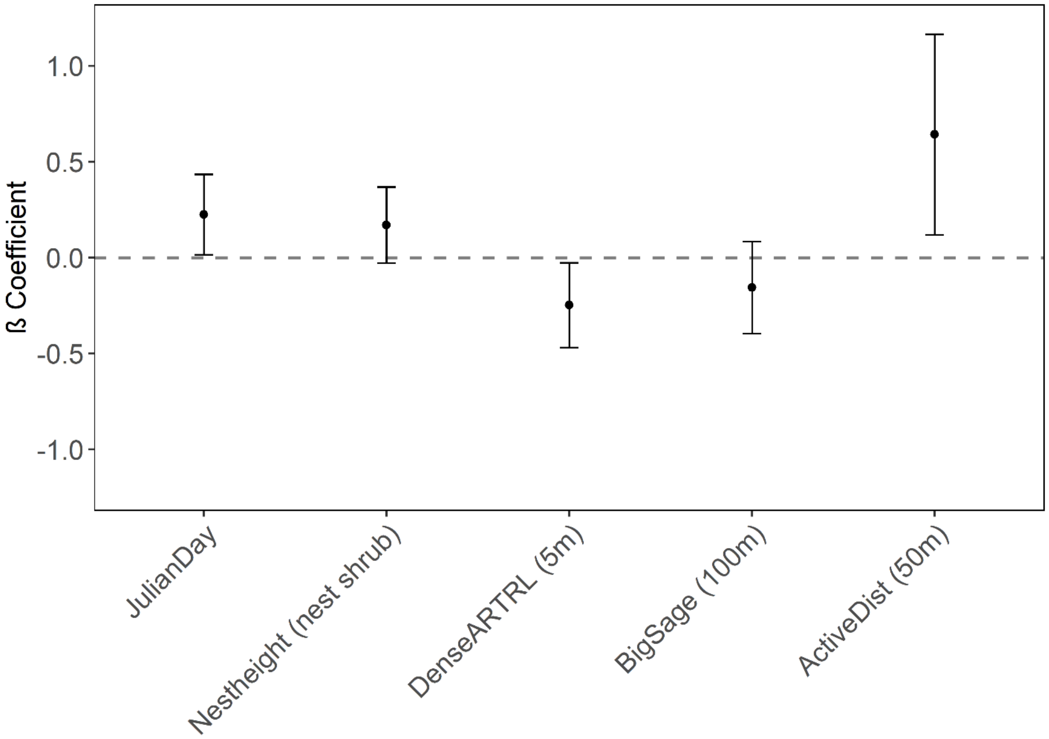


Figure 4.5: Standardized risk ratios and associated 85% confidence intervals for all covariates that were predictive of Brewer's sparrow nest survival in northeastern Wyoming, USA, 2016-2018. JulianDay is a temporal covariate, NestHeight and DenseARTRL (5m) are microhabitat covariates measured in the field, BigSage (100m) and ActiveDist (50m) are spatial covariates derived in Geographic Information Systems (GIS).

4.5 Discussion

Habitat quality is a function of an occupied habitat's conduciveness to survival and reproduction (Hall et al. 1997). Therefore, the effectiveness of reclamation as a mitigation measure should be gauged not only by occurrence of an animal in a reclaimed habitat but also by fitness outcomes. We found that survival of Brewer's sparrow nests was influenced by factors at multiple spatial scales. At a local scale, post-development reclamation reduced a reproductive stressor that was acting on Brewer's sparrow nesting in the active oil and gas development area. Covariates representing sagebrush density and canopy cover were positively related to Brewer's sparrow nest survival at more than one scale, emphasizing the reproductive benefits of unfragmented sagebrush stands to Brewer's sparrow populations.

Microhabitat choices, such as nest placement, are expected to be adaptive and; therefore, be positively correlated to fitness rates (Latif et al. 2012, Chalfoun and Schmidt 2012). We conducted a companion study concurrently at the same study site that examined nest-site selection in Brewer's sparrows (Barlow et al. 2019). This study found that Brewer's sparrow were selecting microhabitat characteristics such as greater visual obstruction surrounding the nest site and taller, more vigorous, sagebrush shrubs for nesting (i.e., greater live foliage and branching density; Barlow et al. 2019). Given the importance of these microhabitat features to the nest site selection process (Barlow et al. 2019), we included these variables in this assessment of the nest survival process. Nest survival was not correlated with the microhabitat characteristics that were supported in our nest-site selection analyses and only two microhabitat covariates were supported in our nest survival modeling, the density of live sagebrush surrounding the nest and the height of the nest bowl in the nest shrub. These findings suggest a potential mismatch between Brewer's sparrow nest-site selection preferences and nest survival outcomes (Latif et al. 2012, Chalfoun and Schmidt 2012). On possible explanation is the adaptive peak hypothesis that suggests nest-site selection may not be correlated with fitness because birds occupy nest sites that minimize predation risk (i.e., achieving an "adaptive peak"). Therefore, this hypothesis suggests that it may be difficult to detect relationships among microhabitat characteristics that should minimize predation (e.g., concealment) because the range of natural variation within which birds place their nests is constrained. However, there are multiple options that maximize reproductive fitness in birds and nest survival is just one of these fitness metrics (Chalfoun and Schmidt 2012). The availability of food resources for the high-quality offspring, that are more likely to survive to adulthood, could be driving microhabitat selection more than predation risk (e.g., microhabitat characteristic related to concealment), for example (Chalfoun and Schmidt 2012).

We found that the density of sagebrush shrubs surrounding a nest were positively correlated with nest survival. At a similar microhabitat scale, Chalfoun and Martin (2007), at an identical microhabitat scale, found that as the density of potential nest shrubs (sagebrush shrubs of similar height and crown width as shrubs used for nesting) increased the Brewer's sparrow nest predation risk decreased. Our results suggest that nests constructed higher in the nest shrub were at greater risk of predation. Brewer's sparrow nests higher in the nest shrub likely had less overhead concealment which may increase the likelihood of being discovered by avian predators. Unfortunately, few studies of shrub-nesting passerines have quantitatively assessed the impact of nest height on the probability of survival (but see Latif et al. 2012). Avian predators known to depredate Brewer's sparrow nests were present in our study area including blackbilled magpies (*Pica hudsonia*) and loggerhead shrikes (*Lanius ludovicianus*; Vander Haegen et al. 2002, Hethcoat and Chalfoun. 2015*b*, Barlow et al. 2020).

At a larger scale (100m radius), Brewer's sparrow nests were more successful in areas with higher mean sagebrush canopy cover which represented more contiguous sagebrush stands. Chalfoun and Martin (2007) found increased number of nesting attempts per Brewer's sparrow pair with increased shrub cover (primarily sagebrush shrubs) within approximately 300m of the nest. Nest survival of a larger, ground-nesting bird, the greater sage-grouse (*Centrocercus urophasianus*), also benefits from greater sagebrush cover surrounding nest sites. Sage-grouse nests in our study area were more likely to be successful if the surrounding habitat (~340m radius) had more sagebrush canopy cover (Kirol et al. 2015*b*). The reduced predation risk of Brewer's sparrow nests in areas with greater amounts of sagebrush highlights the importance of sagebrush reestablishment in reclamation areas. Yet, the long-term prospects of sagebrush recovery in disturbed habitats are uncertain. For instance, natural sagebrush reestablishment (i.e., without planting), on reclamation surfaces in our study area will likely take 80 to 125 years (Davies et al. 2013, Avirmed et al. 2015, Rottler et al. 2018). Thus, some level of impact of oil and gas development on Brewer's sparrow nest survival will also likely persist for a similar timeframe until the disturbance scars have filled in with sagebrush.

Predator-prey dynamics are complex and context-specific. The relationships among energy-related habitat modification and nest survival vary across ecosystems, infrastructure types, and development intensities (sensu Francis et al. 2009 and Bernath-Plaisted and Koper 2016). In sagebrush ecosystems, nest survival rates of ground- and shrub-nesting birds tend to be higher in undisturbed habitats when compared to habitats that have been modified by energy development activities (Heathcoat and Chalfoun 2015*a*, Kirol et al. 2015*b*). At the broadest spatial scale we assessed (i.e., nest-searching plots within different treatments), we found no evidence of differences in nest survival between nests that were within the energy development field, both active and reclaimed treatments, and those in our control. Further, we did not find a difference in nest survival between plots in the active and reclamation development areas. The oil and gas development in our study area was in the production phase and had been in place for approximately 8 years at the beginning of the study. The amount of human activity and vehicle traffic is at its peak when oil and gas fields are first being developed and subsides once the wells are drilled and the infrastructure is in place (Ingelfinger and Anderson 2004, Sawyer et al. 2009). In our study, active wells were generally monitored by vehicle every 1-2 days. Gilbert and Chalfoun (2011) did not observe a decline in Brewer's sparrow abundance in response to greater well densities. Similar to our active treatment, their study area experienced low traffic volumes of about 5 vehicles per day (Gilbert and Chalfoun 2011). Therefore, it is possible that the unexpected similarity across sites could have been influenced by reduced human activity associated with the active oil and gas sites in our study (Barlow et al. 2020).

At a more localized scale (50m radius), we detected a relationship between the amount of active disturbance and nest survival. The likelihood of a Brewer's sparrow nest being depredated increased when the physical footprint of active disturbance increased beyond a certain level (~15% active disturbance). Nest survival did not appear to be influenced by exposure to active disturbance below 15%; however, once active disturbance surpassed this level, nest predation risk began to increase and increased more dramatically when disturbance exceeded 30% of the surrounding habitat patch. This finding suggests there is a level of active disturbance beyond which nest predators are either more abundant or more efficient at discovering nests. Although at a much larger scale (1-km^2 area), nest predation risk in sagebrush breeding songbirds increases as the physical footprint of energy disturbance increases (Heathcoat and Chalfoun 2015*a*). Heathcoat and Chalfoun (2015*a*) demonstrated that with every percent (1 hectare) disturbance within a 1-km^2 area the probability of Brewer's sparrow nest survival decreased by 1.3% and the probability of Sage Thrasher nest survival decreased by 3.2%. Using video monitoring at nest sites and predator surveys, they attribute the elevated nest predation rates to an increased abundance and a different assemblage of nest predators associated with increasing energy disturbances (Heathcoat and Chalfoun 2015*b*).

The majority of Brewer's sparrows in the active treatment area (~80%) nested in sagebrush patches that were exposed to ≤15% disturbance and the average distance from active disturbance edge was 60m. Assuming an average Brewer's sparrow territory size of 0.25 hectares and assuming that nests were generally positioned more centrally within territories, rather than at the edge of the territories (Rotenberry et al. 1999, Harrison et al. 2009), 66% of the nests in the active treatment had no anthropogenic disturbance within their territories. That is, 66% of nests were farther than 30m from active edge. This nest distribution pattern suggests some avoidance of active disturbance by Brewer's sparrow when choosing nest sites. The pattern we observed of nest placement farther from active disturbance likely contributed to the lack of strong support for the relationship we detected between the amount of active disturbance and nest survival. This is reflected in the widening confidence intervals in Figure 4.3 as disturbance levels increase and the data becomes thinner (i.e., there fewer nests to inform the survival model at these higher active disturbance levels). Other species of shrub and grassland birds also avoid anthropogenic development features at scales similar to the territory size of each species (Bayne and Dale 2011, Ludlow et al. 2015, Thompson et al. 2015). Ludlow et al. (2015) found that Baird's sparrows (*Ammodramus bairdii*), a grassland specialist, selected nest sites at least 100m from well access roads which corresponds to their territory size. Therefore, most often Baird's sparrows were selecting nesting territories that did not overlap roads or road edges.

Birds will alter their nest site choices in response to predator pressure across scales (Peluc et al. 2008, Lima 2009). Recognition by Brewer's sparrows of increased risk of nesting in areas with higher levels of active disturbance may explain why the majority of nest sites in the active development area were in sagebrush patches that had less surrounding disturbance. Harrison and Green (2010) found that previous reproductive success was highly correlated with Brewer's sparrow territory choices. Seventy-one percent of returning Brewer's sparrows that had successful nests the previous year returned to the same territory while only 28% of birds that were unsuccessful the previous year returned to the same territory (Harrison and Green 2010).

The pattern of nest site placement relative to reclamation was very similar to the active treatment area. Nest sites in the reclamation treatment were primarily in less disturbed areas with only 17% of nests in sagebrush patches with higher levels of disturbance (15-45% disturbance) within 50m and 78% of nest territories (i.e., 0.25 hectares or 30m radius) did not contain any reclamation. The consistency in the nest distribution suggests that when choosing territories Brewer's sparrow are responding similarly to active disturbance and reclamation. No other research has examined sagebrush songbird responses to reclamation; however, Carlisle et al. (2018*a*) found that Brewer's sparrows nested approximately 35m from mowed sagebrush edges. The mowing treatments created edges and surfaces similar to our reclamation sites in that the majority of mature sagebrush in mowed areas was removed but grasses and forb ground cover remained (Carlisle et al. 2018*a*). Similar to our reclamation treatment, the mowing disturbance fragments sagebrush stands and increases edge but was not associated with devegetated surfaces, persistent human activity, and infrastructure as in our active oil and gas areas.

Despite the similarities in the spatial distribution of nests throughout both active and reclamation areas, our findings provide some evidence that nest predation risk differed. Nesting in sagebrush patches with >15% disturbance appeared to be maladaptive in active areas but inconsequential to nest survival in reclamation areas. That is, when we applied our active disturbance survival model to reclamation there was no relationship between Brewer's sparrow nest survival and the physical footprint of reclamation. This finding provides evidence that, at a local scale, removal of oil and gas infrastructure and the associated activity had a positive influence on Brewer's sparrow nest survival in the reclaimed treatment area. Similarly, Carlisle et al. (2018*a*) found that vicinity to a mowed treatment was not negatively correlated with Brewer's sparrow nest survival and nests closer to mowed edges actually had marginally higher survival rates.

Indicator species are used to "indicate" condition or a response to environmental stressors that may apply to other species with similar ecological requirements (Neimi and McDonald 2004). The relationships we detected between Brewer's sparrows nest survival and oil and gas development and reclamation, as well as sagebrush cover, are likely indicative of other songbird species breeding in these same sagebrush habitats. At the broader spatial scales, these species are exposed to similar environmental conditions and similar nest predation pressures as Brewer's sparrows (Vander Haegen et al. 2002, Heathcoat and Chalfoun 2015*b*). Other songbird nests that we recorded in our nest-searching plots included lark bunting (*n* = 17), lark sparrow (*n* = 22) and vesper sparrow (*n* = 12). These species all built open-cup nests on the ground under the shelter of sagebrush shrubs (Barlow et al. 2019, Fedy and Kirol *unpublished data*). In sagebrush habitats in Washington and Wyoming, lower nest survival in habitats fragmented by human activities was consistent across a suite of ground- and shrub-nesting songbirds (e.g., Brewer's sparrows, sagebrush sparrows [*Artemisiopiza nevadensis*], sage thrashers). The increased nest predation in these fragmented habitats was attributed to rodent nest predators achieving greater abundance in these areas (Vander Haegen et al. 2002, Hethcoat and Chaloun 2015*b*, Sanders and Chalfoun 2019). Therefore, we suggest that because Brewer's sparrow nests are experiencing greater predation risk in sagebrush patches with less sagebrush cover and higher levels of active disturbance, it is probable that these co-occurring songbird species were also experiencing greater nest predation risk.

Our research is the first to explore a fitness response to oil and gas reclamation in a sagebrush breeding songbird. We demonstrated that sagebrush canopy cover and composition is important to Brewer's sparrow reproductive success at the nest site and surrounding areas. We did not find direct evidence that fragmentation of sagebrush habitat effected nest survival rates at a landscape scale. Brewer's sparrow generally avoided reclamation surfaces similar to active disturbance; however, nest survival was affected differently by the two types of disturbance with the greater negative impact on survival in the active areas. At a local scale, we found different nest survival responses in the active and reclamation treatment areas, providing some evidence that infrastructure and human activity associated with active disturbance may be more influential on Brewer's sparrow nest predation risk than the physical footprint of disturbance. It is important to emphasize that we identified a short-term fitness response to reclamation but the legacy of oil and gas disturbances in sagebrush areas will remain for decades. That is, successful reclamation of sagebrush landcover—restoring sagebrush to its pre-disturbance size and structure—is a long-term process (Baker 2011, Avirmed et al. 2015). Given the absence of sagebrush directly within the disturbance scars, it is unsurprising that we did not find a single Brewer's sparrow nest in reclamation areas ≤ 5 years after reclamation took place. Because sagebrush reclamation is a long-term process, studies on decades old reclamation areas are needed to provide a more complete understanding of bird responses to mitigation. Our research demonstrates scale-dependent nest survival relationships and reiterate the importance of looking at multiple scales when assessing fitness outcomes (Stephens et al. 2004, Ibáñez-Álamo et al. 2015).

Chapter 5

Individual variation in the response of a declining population of birds to anthropogenic disturbance in an established energy field

5.1 Abstract

Habitat selection in animals occurs across spatial scales from selection for broad geographic areas to fine-scale habitat components. Therefore, the scale of interest must dictate the spatial extent of the area considered as available to the animal and availability should be based on biologically realistic movements of that species or individual. Habitat selection studies are usually conducted at a population level. Habitat selection analyses at an individual level can reveal patterns in selection that are not apparent when using a population-level approaches. Advances in transmitter technology, allowing for high-resolution location and movement data, and data analyses allowed us to explore individual-level movements, space use (e.g., home ranges) and habitat selection of female greater sage-grouse (*Centrocercus urophasianus*) that raised chicks (brood-rearing sage-grouse) in an energy development landscape. To evaluate habitat selection and avoidance behaviors, we used integrated step selection analysis (iSSA) that permit the quantification of the effects of environmental and anthropogenic covariates on the movement and selection process simultaneously. On average, brood-rearing female sage-grouse established home ranges in areas with a majority of the home range comprised of sagebrush landcover (mean = 77.4%) and a minimal proportion of the area comprised of anthropogenic surface disturbance (mean = 3.5%). We did not find a difference in space use (e.g., home range area) and movements (e.g., step lengths) between individuals exposed to higher proportions of anthropogenic disturbance (high-exposure females) and those exposed to lower proportions of disturbance (low-exposure females) within their home ranges. Individual-level selection analyses helped us uncouple some aspects of energy development that influence habitat selection that likely would not have been detected at broader spatial scales. Brood-rearing females consistently selected for natural vegetation and avoided disturbed surfaces, including reclamation surfaces, at fine spatial scales. Power line visibility generally led to avoidance behavior; however, much shorter (3m) wells structures generally did not. We found that individual variability was partially explained by age (adult or first year), or previous experience of the landscape. Adults were more likely than first year females to demonstrate avoidance of energy features and adults were also less likely than first year females to establish home ranges in areas with energy infrastructure. Our results do not support individual uniformity in brood-rearing sage-grouse and reiterate the importance of accounting for, or at least recognizing, individual variability in population-level modeling efforts.

5.2 Introduction

The selection of habitats by animals can be viewed as a hierarchical process that results in the disproportionate use of some habitat components and the avoidance of others across multiple scales (Johnson 1980). Fundamental to habitat selection is the implicit assumption that evolution has shaped these behaviors to maximize survival and fitness (Jones 2001). The habitat selection process in animals is often conceptualized as four selection orders (Johnson 1980, Meyer and Thuiller 2006). These orders are nested and progress from the broadest first-order (the geographic range of a species) through the second-order home range of an individual, third-order selection of patches within the home range, and finally the fourth-order representing the selection fine-scale habitat components (Johnson 1980, Meyer and Thuiller 2006). The specific order of selection of interest must dictate the spatial extent of the area considered as available to the animal and availability should be based on biologically realistic movements of that species or individual (Jones 2001, Meyer and Thuiller 2006, Avgar et al. 2016). There is a long history of habitat selection analysis and typically, these studies aim to predict the habitat selection behavior of a species by modeling the aggregate responses of multiple individuals (i.e., population-level inference) across an area of interest.

However, animals exhibit individual variation in movement, habitat selection and space use (Durell 2000, Hertel 2020, Shipley et al. 2020). Individuals from the same species and population may adopt different habitat-use strategies and these differences can be influenced by factors such as social status (e.g., exclusion of subdominant individuals from preferred habitats) or by an individual's exposure to particular habitats based on availability or previous experience (Durell 2000, Leclerc et al. 2016). Individual variation in habitat-use strategies can, of course, be studied across multiple scales of selection. An animal’s home range (i.e., second-order) represents the distribution of an animal during a specified time period or life stage (Kernohan et al. 2001) and home range size can be affected by biotic interactions and intrinsic factors. Biotic interactions might include territorial behavior and intrinsic factors might include the sex or age of the individual (Börger et al. 2008). At a finer scale, it is common for individuals to vary in their selection of particular habitat patches and responses to particular habitat features (Goss-Custard and Durell 1983, Durell 2000). Therefore, it is possible for individual variation to manifest across multiple scales and understanding this variation can reveal important aspects of a species’ ecology, expand on our previous understanding of habitat selection, and potentially inform management and conservation of a species.

Our capacity to refine our understanding of habitat selection from population-level assessments to modeling individual behaviors has been driven by technological advancements in both data collection (i.e., transmitter and tracking technologies; Kirol et al. 2020*b*) and data analyses (Avgar et al. 2016). This permits the quantification of the effects of environmental and anthropogenic covariates on the movement and selection process simultaneously. Habitat selection and movement processes are interlinked because habitat and availability affect an animal's movements (e.g., an animal has to move farther to take advantage of resources that are farther away) and an animal's movement capacity affects its habitat use patterns (e.g., an animal can only use resources that it can realistically travel to; Forester et al. 2009, Avgar et al. 2016, Prokopenko et al. 2017). Integrated step selection analyses (iSSA) use a matched design where each individual location at each time point is associated with a specific set of random locations within a spatial domain limited by that individuals observed movements. Therefore, iSSA allow for a realistic assessment of what is truly available to that individual at that time (Thurfjell et al. 2014, Avgar et al. 2016, Muff et al. 2020). In combination with high-frequency animal relocation data, iSSA models allow us to explore individual behavioral differences related to habitat selection and movements (Dickie et al. 2020, Muff et al. 2020). Quantification of habitat selection at an individual level can reveal patterns in selection that are not apparent when using a population-level approach (Muff et al. 2020).

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) has been the subject of many habitat selection studies across its range in sagebrush steppe habitats throughout the intermountain west of North America. These past studies have quantified habitat selection behavior of sage-grouse across their annual cycle at a population-level and; thus, provide a foundation for the examination of more refined, individual-level, assessments of habitat selection. Our study focused on a population of sage-grouse in the Powder River Basin (PRB) in northeastern Wyoming. Multiple population-level habitat selection studies were conducted during the onset of oil and gas development in this region (Walker et al. 2007, Doherty et al. 2008). To date, the PRB sage-grouse population has persisted in this energy development landscape; however, it has declined considerably over the last three decades and the outlook for this population is uncertain (Garton et al. 2011, Taylor et al. 2013, Fedy et al. 2017). Persistence of this population is critical to maintaining genetic connectivity to populations in North Dakota, South Dakota and Montana, USA (Cross et al. 2018, Row et al. 2018).

The survival of sage-grouse chicks from hatch to independence is an important component of overall population performance (Taylor et al. 2012). Additionally, female sage-grouse with chicks can be particularly sensitive to anthropogenic disturbances and sage-grouse chicks have lower survival rates in landscapes altered by energy development (Aldridge and Boyce 2007, Lebeau et al. 2017, Kirol et al. 2020*a*). Previous research has demonstrated that at the second order of selection brood-rearing females will avoid anthropogenic disturbance when there is suitable undisturbed brood-rearing habitat available to them (Kirol et al. 2015*a*, Lebeau et al. 2017). We used iSSA to explore movements and habitat selection within the home ranges of female sage-grouse that successfully raised chicks (i.e., brood-rearing females) which corresponds to the third-order of selection (Johnson 1980). Our study site was located primarily within an oil and gas development and allowed us to assess finer scale effects of environmental and anthropogenic covariates on individual brood-rearing sage-grouse (Thurfjell et al. 2014). Female sage-grouse are likely under strong selection pressure to balance predation risk to themselves and their chicks with the need to provide foraging opportunities and high-quality nutrition for their dependent chicks (Hagen 2011, Smith et al. 2018).

Studies have demonstrated that avoidance of energy disturbance reduces the spatial distribution of sage-grouse because sage-grouse avoid otherwise suitable habitat after infrastructure is introduced (termed functional habitat loss; Aldridge and Boyce 2007, Naugle et al. 2011). In addition, avoidance behavior tends to increase with increasing densities of energy development (Aldridge and Boyce 2007, Walker et al. 2007, Naugle et al. 2011, Kirol et al. 2015*a*). However, despite multiple studies on the impacts of energy development (both renewable and non-renewable) on sage-grouse, the specific mechanisms that drive avoidance behavior are not well understood (Naugle et. al. 2011). For instance, is avoidance behavior in oil and gas fields driven primarily by the tall structure components of development, such as wells and power lines, or primarily by habitat loss (i.e., the physical footprint of development), or is it the aggregate of all these components that drive avoidance? Furthermore, we have less information on long term avoidance because most research has been conducted when the energy disturbance was first occurring (i.e., development phase). Much less research has focused on the production phase when construction has largely subsided and there is less human activity (Sawyer et al. 2009, Naugle et al. 2011, Holloran et al. 2015).

We used sage-grouse raising chicks in an established energy field to evaluate several interrelated research questions. First, are there differences in home range size and movements of brood-rearing sage-grouse in highly developed areas compared to those in less developed areas? Second, does third-order selection analyzed at the individual level suggest similar habitat selection patterns as analyses conducted at a population level? Third, are there differences in habitat selection or avoidance behavior of females exposed to higher densities of oil and gas disturbance compared to those exposed to lower densities? Fourth, are there differences in habitat selection or avoidance behavior related to the age of individuals (e.g., first year versus adult)? Finally, can individual-level third-order selection analyses help us uncouple the specific components of oil and gas development (e.g., well structures or power lines) that may be driving avoidance behavior?

5.3 Methods

5.3.1 Study area

Our study area was located in sagebrush-steppe habitat in northeastern Wyoming, USA, within the PRB region (44.2603ºN, -106.3095Wº; Figure 5.1). Dominant shrubs included big sagebrush (*Artemisia tridentata*) and silver sagebrush (*A. cana*), black greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* and *Ericameria* spp.). Common native grasses included blue grama (*Bouteloua gracilis*), and bluebunch wheatgrass (*Pseudoroegneria spicata*). Common invasive grasses include cheatgrass (*Bromus tectorum*) and Japanese brome (*B. japonicas*). In addition to sage-grouse, other bird species occupying sagebrush stands in our study area included: Brewer's sparrow (*Spizella breweri*), Brewer's blackbird (*Euphagus cyanocephalus*), lark bunting (*Calamospiza melanocorys*), lark sparrow (*Chondestes grammacus*), loggerhead shrike (*Lanius ludovicianus*), mourning dove (*Zenaida macroura*), sage thrasher (*Oreoscoptes montanus*), spotted towhee (*Pipilo maculatus*), vesper sparrow (*Pooecetes gramineus*) and western meadowlark (*Sturnella neglecta*; Barlow et al. 2020).

Our study area primarily contained coal-bed natural gas (CBNG) disturbance. CBNG wells were developed at a density of 3.1 well pads per km^2 (80-acre spacing; Walker et al. 2007). On average, CBNG well pads required the clearing of 0.5 ha of natural vegetation per pad. This estimate does not include access roads of various lengths and other supporting infrastructure (e.g., compressor stations and pipelines). In addition to well pads, CBNG development at this spacing generally requires 2-7 km of road construction per km^2 (Walker et al. 2007). CBNG wells are about 3 m tall while other supporting infrastructure like compressor stations are much taller (5-8 m). Livestock ranching was another major land use in the area. Elevation ranged between 1260 – 1450 m. Detailed descriptions of the region and CBNG development patterns are available in previous publications (e.g., Walker et al. 2007, Kirol et al. 2015*b*).

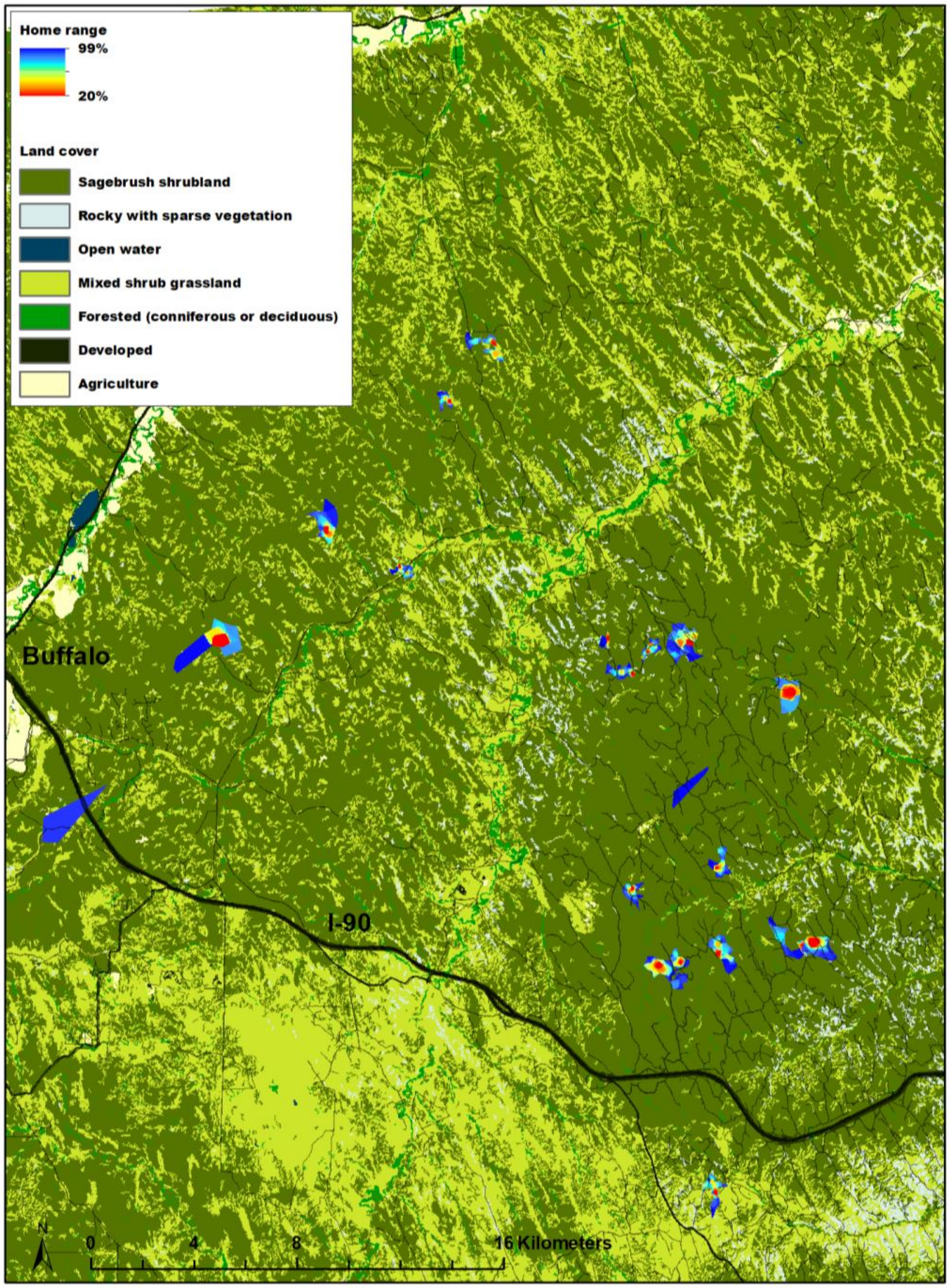


Figure 5.1: Map of study area land cover and 99% home ranges for brood-rearing greater sage-grouse (*n* = 18; 2017-2019) in northeastern, Wyoming, USA. Home ranges estimated using adaptive sphere-of-influence local convex hull nonparametric kernel method (*a*-LoCoH). The red areas are the lower home range percentiles (~ 20%) or 'core areas' within each home range.

5.3.2 Captures and monitoring

We captured female sage-grouse in 2017–2019 using mobile CODA net launchers and nighttime spot-lighting with hoop nets (Wakkinen et al. 1992, Sutphin et al. 2018). We targeted capturing at sage-grouse leks within and on the periphery of a large natural gas field in the spring and searched for female sage-grouse within and adjacent to the natural as field in the fall. We aged females as yearlings (first breeding season) or adults (second breeding season or older) based on the shape and condition of the outermost wing primaries, the outline of the primary tail feathers, and coloration of undertail coverts (Eng 1955, Dalke et al. 1963). We termed first year females 'inexperienced' and second year or older females 'experienced'. We fitted females with rump-mounted 13-g solar LRD (long range download) GPS-UHF (ultra-high frequency) GPS loggers (Ecotone Telemetry Lech Iliszko, Sopot, Poland) with independent 10-g VHF transmitters. Kirol et al. (2020*a*) provides a detailed description of the tracking devices (hereafter tags) and tracking procedures. The tags collected GPS locations every 4 hours. All research was conducted with approval from the University of Waterloo (Animals for Research Act and the Canadian Council on Animal Care guidelines, AUPP# 16-06).

We monitored tagged female sage-grouse weekly from April through August. Females that successfully hatched nests were considered brood-rearing females. At each visit, we determined if the female was still with her brood (i.e., brood-rearing) by visually locating the chicks with binoculars or by observing brooding behavior (e.g., distraction displays, feigning injury, clucking, and hesitation to flush). We considered a brood successful if we confirmed the female was with ≥1 chick at this date. We confirmed brood fate at 40 days post-hatch because the majority of chick mortality has occurred by this age and chicks are more likely to survive to breeding age after this time (Gregg et al. 2007). We used a FLIR Scout II-640 Thermal Monocular (FLIR Systems, Inc. Wilsonville, Oregon, USA) and spot-lighting (Walker et al. 2006, Dahlgren et al. 2010) to verify brood fate at 40 days. Our study only included locations from females that were caring for broods from nest hatch (0 days) to ~40 days.

We estimated the error of our tags by placing two tags at fixed locations in our study area. The tags were set to gather location data every 30min for a one-month period. We calculated location error as the median linear distance between tag recorded GPS points and the true tag location as determined by placing a hand-held Garmin 64s GPS unit (Garmin International, Olathe, Kansas, USA) at the tag location and averaging waypoints for 15 min to improve waypoint accuracy.

5.3.3 Movement data

Tags were set to collect GPS locations every 4 hours (6 locations/24-hr period). High-resolution movement data (i.e., frequent relocation intervals) can be highly autocorrelated, resulting in poor estimates of home range area and biased model and error terms (Calabrese et at. 2016). Prior to estimating home ranges and modeling our brood-rearing data we assess autocorrelation with the continuous-time movement modeling ('ctmm') package (Calabrese et at. 2016). With the ctmm package, we inspected the autocorrelation structure of relocation data for each individual using variograms. Autocorrelation was not an issue with 4-hour relocation intervals, therefore we did not resample our data.

5.3.4 Spatial covariates

All of the environmental covariates we included in our models were relevant to sage-grouse brood-rearing ecology and supported by previous studies on sage-grouse habitat selection during brood-rearing (Table 5.1). Vegetation cover variables including, sagebrush cover, sagebrush height (cm) and herbaceous cover were derived from the 2016 shrubland layers (30-m resolution) available through the U.S. National Land Cover Database (Xian et al. 2015, Yang et al. 2018). The importance of sagebrush cover and herbaceous cover to brood-rearing sage-grouse has been demonstrated by many studies (e.g., Aldridge and Boyce 2007, Cassaza et al. 2011, Kirol et al. 2015*a*). Brood-rearing sage-grouse also avoid rough terrain at landscape and local scales (Dinkins et al. 2014*a*, Fedy et al. 2014, Kirol et al. 2015*a*). We calculated terrain roughness (vector roughness measure [VRM]) at a 30-m resolution using a 10-m digital elevation model (Sappington et al. 2007). Low VRM values indicate flat terrain while high values indicate rugged terrain. Normalized difference vegetation index (NDVI) is a measure of live green vegetation or 'greenness' (Robinson et al. 2017). NDVI has proved predictive of sage-grouse habitat selection during brood-rearing and can be related to population productivity (Blomberg et al. 2012, Smith et al. 2018). We calculated time-varying NDVI covariates using dynamic 30-m resolution NDVI products generated every 16 days (Robinson et al. 2017). For each year (2017–2019), we averaged four NDVI composites that temporally overlapped the brood-rearing period in our study, approximately May 15th to July 31th. The highest NDVI values, in our study area, were indicative of live herbaceous ground cover with little to no sagebrush cover. Low NDVI values were indicative of bare ground.

Habitat modification and infrastructure associated with energy development can influence habitat use patterns during all sage-grouse life stages (Naugle et al. 2011). Development of gas reserves requires the clearing of vegetation for well pads and supporting infrastructure such as roads, wastewater holding reservoirs, facilities and pipelines (sensu Walker et al. 2007, Finn and Knick 2011, Walker et al. 2020).

We created covariates related to natural gas development that fell into two broad categories: 1) natural vegetation removal (i.e., disturbance) and; 2) infrastructure features (Table 5.1).

We obtained disturbance layers that were digitized (head's up digitizing at a min. 1:5000 screen resolution; https://ddct.wygisc.org/ddct-procedure.aspx) following the Disturbance Calculation Tool (DDCT) process used to quantify disturbances in the sagebrush ecosystem in Wyoming, USA (State of Wyoming 2019). With the DDCT disturbance data, we created surface disturbance layers at a 1-m resolution that represented active and reclaimed disturbances that quantified the direct loss of natural vegetation. Active disturbances were areas stripped of vegetation that remain devegetated or are partially vegetated with interim reclamation seed mixes (e.g., disturbance areas surrounding active wells pads; Kirol et al. 2020*a*). Examples of active disturbance in our study area included graveled access roads, well pads and compressor sites (Figure A3). Reclamation surfaces included areas without above ground infrastructure that had been revegetated with reclamation seed mixes but were largely devoid of sagebrush (Kirol et al. 2020*a*). Reclamation surfaces in our study area were primarily reclaimed well pads, access roads and pipeline corridors (Figure A4). Active disturbance and reclamation covariates were quantified as the percent of disturbance per 30-m pixel on the landscape (0-100% active disturbance or reclamation). We also used the DDCT layer to produce a layer that categorized landscape pixels into discrete classes of undisturbed natural vegetation or disturbed (active + reclamation). We termed this covariate Landcover factor. In some cases, categorical habitat classifications can be better at detecting selection and movement behaviors (Thurfjell et al. 2014).

Infrastructure covariates included power transmission lines (hereafter power lines), CBNG features (e.g., wells and compressor stations) and man-made reservoirs (Table 5.1). Power line data were obtained from the Powder River Energy Corporation and active and plugged and abandoned well data were obtained the Wyoming Oil and Gas Conservation Commission (http://wogcc.wyo.gov/). Well data included location, type, status, status date and spud date (initiation of drilling). Man-made reservoirs were extracted from the DDCT disturbance layers. All infrastructure was verified, and in some cases corrected, using ESRI world imagery (https://services.arcgisonline.com/arcgis/rest/services/World_Imagery/MapServer)

Visible structures can be negatively associated with sage-grouse habitat use and chick survival (Aldridge and Boyce 2007, Kirol et al. 2015*a*, Lebeau et al. 2019). We developed viewshed surfaces to determine the number of infrastructure features and power lines that were visible by sage-grouse from any given pixel on the landscape (Table 5.1). Power lines can uniquely influence habitat use and fitness rates in sage-grouse (Gillian et al. 2013, Gibson et al. 2018, Lebeau et al. 2019). Therefore, we developed a viewshed covariate for power lines and a second viewshed covariate for all other structures in our study area. We calculated how many structures were visible within a 1.0 km viewshed distance (Kirol et al. 2015*a*, Lebeau et al. 2019). Each type of structure received a specific height above ground value. For instance, well structures were given a height of 3 m, compressor or pumping stations a height of 5 or 8 m and power lines a height of 27 m (Figures A5-A7). The height values were based on the average heights of these structures measured in the field.

Mesic habitats adjacent to water are often selected by brood-rearing sage-grouse but these areas can also be riskier for sage-grouse chicks, likely due to increased predation (Aldridge and Boyce 2007, Connelly et al. 2011*b*, Kirol et al. 2015*b*). We were interested in fine-scale relationships with wetter habitats surrounding man-made reservoirs in our study area. We transformed continuous distance variables using a decay function ($e^{-d/\alpha}$) where d was the distance in meters from each pixel to man-made reservoir edge which allowed the effect to decay as distance to the reservoir increased (Fedy and Martin 2011). We used 100 as the decay constant (α) which decays to zero at ~300 m (Walker et al. 2016).

The resolution or scale of the spatial covariates used in our analysis were informed by the median location error of our tags (median = 14.46 m). To properly account for tag error the finest resolution assessed was a 30 x 30 m pixel or a 15-m radius circular scale. Spatial variables were processed using ArcGIS 10.7.0 – 10.7.1 (http://www.esri.com) and R statistical software (R Core Team 2020).

Table 5.1: Covariates that were assessed in our integrated step selection analysis (iSSA) models used to model habitat selection in brood-rearing female sage-grouse. The movement covariate cos_ta was present in all individual models. The environmental covariates that had the most support across individual models formed the base environmental model. The anthropogenic covariates were assessed in conjunction with the base model for each individual.

Covariate	**Covariate type**	**Description**
Cos_ta	Movement	Cosine of the turn angle that describes the directionality of movements
Sage	Environmental	% sagebrush cover (all *Artemisia* spp.; Xian et al. 2015)
Sage + SageQ	Environmental	Quadratic form of % sagebrush cover
ShrubHeight	Environmental	Shrub height (cm; all woody stemmed shrubs; Xian et al. 2015)
ShrubHeight + ShrubHeightQ	Environmental	Quadratic form of shrub height
NDVI	Environmental	Biweekly Normalized Difference Vegetation Index (NDVI) representing live green vegetation averaged over study period (May 15th to July 31th each year; Robinson et al. 2017)
NDVI + NDVIQ	Environmental	Quadratic form of NDVI
Herb	Environmental	% herbaceous cover (consists of grasses, forbs and cacti; Xian et al. 2015)
Herb + HerbQ	Environmental	Quadratic form of % herbaceous cover
VRM	Environmental	Vector roughness measure (VRM; low values indicate flat terrain, high values indicate rugged terrain; Sappington et al. 2007)

Active disturbance	Anthropogenic	% active disturbance (areas stripped of natural vegetation that are associated with infrastructure or access roads)
Reclamation	Anthropogenic	% reclamation (formally active disturbances that have been reclaimed and revegetated with reclamation seed mixes)
Landcover factor	Anthropogenic	Categorical covariate of undisturbed natural vegetation (coded as 0) or disturbed (active + reclamation; coded as 1)
Power line viewshed	Anthropogenic	A count of the number of power poles that were visible from any given pixel on the landscape based on a 1.0 km viewshed distance
Structure viewshed	Anthropogenic	A count of the number of CBNG infrastructure features that were visible from any given pixel on the landscape based on a 1.0 km viewshed distance
Reservoir distance	Anthropogenic	Linear distances to man-made reservoirs transformed using a decay function ($e^{-d/\alpha}$) where 100 was a decay constant (α) and d was the distance in meters from each pixel to the reservoir edge

5.3.5 Home range estimates, home range characteristics and movements

We estimated brood-rearing home ranges using the local convex hull (LoCoH) nonparametric kernel method and, specifically, the adaptive sphere-of-influence LoCoH method (*a*-LoCoH; Getz et al. 2007). We generated 99% *a*-LoCoH home range for each individual.

We quantified the proportion of sagebrush landcover and all anthropogenic disturbance within each individual's home range. All anthropogenic disturbance included any disturbance that replaced natural vegetation (e.g., active disturbance, reclamation and man-made reservoirs). We inspected the 2016 sagebrush cover layer with high-resolution imagery (Google Earth, Google LLC, Mountain View, CA, USA) and determined that 30-m landscape pixels that had sagebrush raster values ≤6%, in our study area, generally contained little to no sagebrush cover. To approximate the extent of sagebrush within home ranges, we created discrete classes of non-sagebrush (raster values = 0–6%) and sagebrush (raster values = 7–36%) pixels. Consequently, pixels classified as sagebrush encompassed a range of sagebrush canopy cover from sparse to dense.

We calculated two movement metrics, step lengths and net-squared displacement (NSD), to explore movement patterns and detect changes in movement behavior (Edelhoff et al. 2016). We generated step lengths (i.e., the distance between the start-point and end-point of a given step) and NSD using the 'move' package; Kranstauber et al. 2020). NSD calculates the squared distance between each location along an individual's track and the its original location. We calculated NSD from each individual's nest.

We plotted NSD against days since the female and chicks left the nest (hatch day) to detect any significant change-points that might be suggestive of a shift from early to late brood-rearing areas during the first 40 days after hatch. Sage-grouse studies have suggested distinct early and late brood-rearing periods that correspond to movements between different habitat types and some research suggests a transition from early to late brood-rearing habitat between14 and 21 days post-hatch (Thompson et al. 2006, Connelly et al. 2011*b*).

To test if sizes of brood-rearing home ranges differed between sage-grouse raising chicks in areas with minimal disturbance and those within a producing CBNG field, we separated female sage-grouse into two groups based on disturbance exposure. Sage-grouse with ≤ 3% disturbance within their home range were grouped as low-exposure hens, while those in areas with > 3% were grouped as high-exposure hens (Kirol et al. 2020*a*). We also tested if there were differences in movement characteristics between low-exposure and high-exposure hens by comparing the step lengths of the individuals in each group. We used a 2-tailed t-test to assess potential differences in home range sizes and step lengths between groups.

5.3.6 Movement linked habitat selection analysis

We used iSSA (‘amt’ package; Signer et al. 2019) to simultaneously model movement and habitat selection of brood-rearing sage-grouse (Avgar et al. 2016). The iSSA establishes an availability domain that corresponds directly to each used location and; therefore, restrains availability to an area the animal could potentially use such as availability corresponding to an individual’s home range (Thurfjell et al. 2014, Prokopenko et al. 2017). Using the iSSA model we compared each used movement step with a set of conditional available steps (*n* = 100) that were randomly sampled from a distribution parameterized based on the observed steps (Avgar et al. 2016). Movement steps were characterized by their length (i.e., step length) and direction defined as the angular deviation (i.e., turn angle) between successive steps. Available steps and turn angles were sampled from a Gamma distribution and a von Mises distribution, respectively (Signer et al. 2019). Environmental and anthropogenic covariates were extracted from the end point of each step to assess the direct effect of anthropogenic and environmental covariates on the selection process (Signer et al. 2019).

Each individual model contained the movement-related covariates including the log of step length (log_sl) and the cosine of the turn angle (cos_ta). The log_sl term is included as a modifier of the shape parameter of the underlying gamma distribution and the cos_ta is used to describe the directionality of an individual’s movement (Signer et al. 2019). We fit a conditional logistic regression model to the data using the ‘survival’ package (Therneau 2020).

To evaluate movement and habitat selection responses to anthropogenic features and habitat alteration we first modeled environmental covariates, in combination with the movement-related covariates, that are known to influence habitat selection during the sage-grouse brood-rearing period. We also considered both linear and quadratic terms for vegetation covariates to allow us to detect selection for intermediate values of these covariates, such as selection for intermediate sagebrush cover (Doherty et al. 2010). All covariates, other than decay distances and the movement-related covariates, were standardized. To assess model support and identify the most informative parameters we relied on Akaike’s Information Criteria (AIC) scores and 85% confidence limits at each stage of the model building process (Burnham and Anderson 2002, Arnold 2010). When environmental variables were correlated ($r \geq |0.70|$), we chose the most informative covariate or covariate representation (i.e., linear or quadratic) based on the degree of AIC support across individual models. The covariates that had the most support across individual models formed our base environmental model (hereafter base model; Scrafford et al. 2018).

We used the base model to assess the relative contribution of each anthropogenic covariate while accounting for environmental variation (i.e., statistical control; Hosmer and Lemeshow 2008). When assessing support for anthropogenic covariates for each individual model we used the same base model and combined it with each anthropogenic covariate of interest (base model + anthropogenic covariate). Anthropogenic covariates that had 85% confidence limits that did not overlap zero were modeled in our final candidate set. Using AIC, the candidate sets were compared to each other and to the base model. The candidate model with the lowest AIC score was identified as the most parsimonious model for that individual. However, if the candidate model was not at least 2 AIC better than the base model, we assumed that the addition of the anthropogenic covariate(s) did not improve model fit (i.e., the anthropogenic covariates were not informative; Arnold 2010). Note, not all individuals were exposed to all anthropogenic covariates of interest. For example, several brood-rearing sage-grouse did not settle in home ranges that were near power lines. When the anthropogenic covariate was not within the availability domain of that individual it was not assessed in the candidate set. We considered anthropogenic covariates to not be within the availability domain if > 95% of available locations contained zero values for that covariate. All analyses were conducted using R statistical software (R Core Team 2020).

5.4 Results

5.4.1 Monitoring

Our analysis included 18 female sage-grouse that we verified successfully raised chicks (i.e., brood-rearing) to 40 days post-hatch (n = 4 in 2017, n = 5 in 2018 and n = 9 in 2019). The mean number of relocations per individual (± SE) was 236.22 ± 2.60 (range = 204–244).

5.4.2 General space use and movement

The average 99% home range size for all individuals was 0.85 ± 0.21 km^2 (range = 0.26–4.02 km^2). The majority of home ranges were immediately adjacent to or included the females nest site (Figure 5.2). For most individuals, NSD from the nest plotted against time showed little variation over the first 40 days after hatch (Figure 5.3). Only two individuals (RAP27 and PAR09) had NSD distributions that signaled pronounced shifts in their movement states. RAP27 moved ~3.5 km on day 5 post-hatch. PAR09 moved ~ 8 km between days 37 and 38 post-hatch (Figure 5.3). NSD plots did not demonstrate any temporally consistent movement shifts across individuals that would suggest movements from early to late brood-rearing areas at a certain day post-hatch (Figure 5.3).

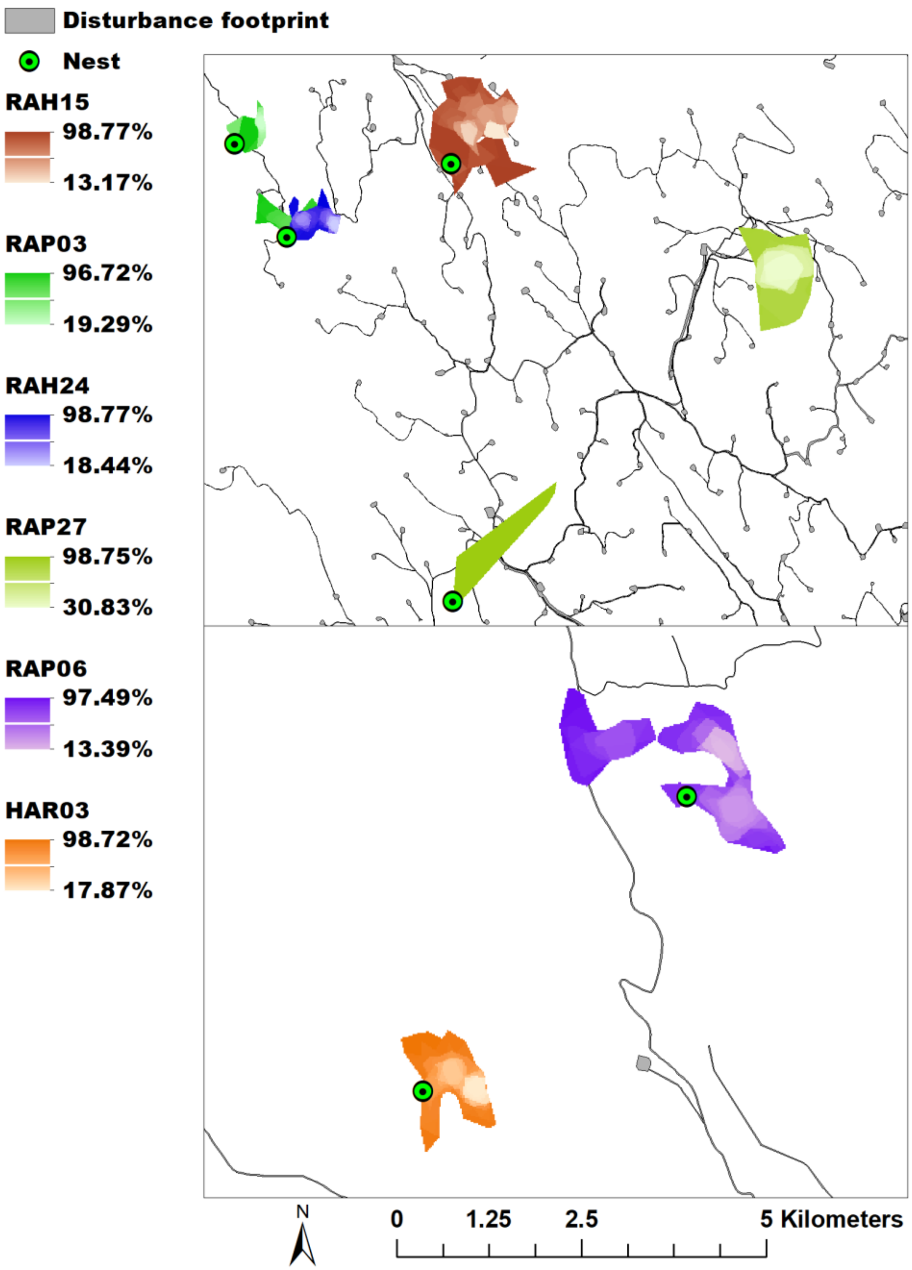


Figure 5.2: Example of 99% home ranges estimated using adaptive sphere-of-influence local convex hull nonparametric kernel method (*a*-LoCoH) for six brood-rearing greater sage-grouse in northeastern Wyoming, USA. Color gradient for each individual indicates ~10 to ~99 percentile isopleths. The lightest areas are the lower home range percentiles (≤ 20%) or ‘core areas’ within each home range.

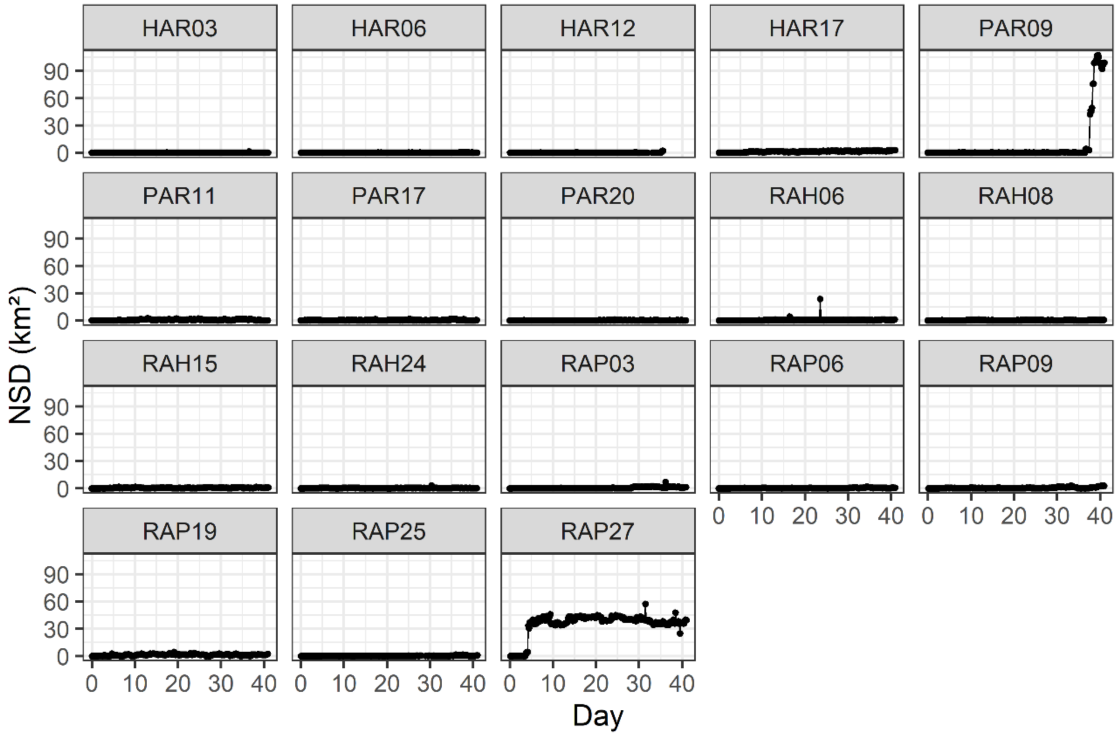


Figure 5.3: Net-squared displacement (NSD) for each individual from its nest site. We plotted NSD against post-hatch days (days since the female and chicks left the nest) to 40 days. NSD allows for detection of change-points that indicate movement shifts to different areas. Movement data is from brood-rearing greater sage-grouse in northeastern Wyoming, USA.

5.4.3 Home range landcover and anthropogenic disturbance

The extent of sagebrush landcover within individual home ranges was never less than 40% (range = 40.28–98.20%). Across individual home ranges, the mean proportion of sagebrush landcover was 77.37 ± 3.36%. The mean proportion of anthropogenic surface disturbance for all home ranges was 3.59 ± 0.75%. The greatest proportion of anthropogenic disturbance for any home range was 14.65%, which was an outlier and twice as high as the second highest proportion of disturbance (6.68%) for any individual. Of the 14.65% disturbance within this individual’s home range, 5.33% was reclamation which was also the highest amount of reclamation surface within any individual’s home range. Seventeen out of the 18 brood-rearing females had at least some anthropogenic disturbance within their home ranges (range = 1.38–14.65%). Of these 17 individuals, seven (41%) had reclamation (range = 0.21–2.76%), in addition to active disturbance, within their home ranges.

5.4.4 Home range, space use and movement comparisons

The mean proportion of surface disturbance within individual home ranges was 1.96 ± 0.28% for low-exposure hens and 5.63 ± 1.38% for high-exposure hens. We did not detect a statistical difference between space use, quantified as home range area, of low-exposure hens ($n = 10$) and high-exposure hens ($n = 8$; $t = 2.31$, df = 10, $P \leq 0.297$). Mean home range size for low-exposure hens was 0.63 km^2 (85% CI: 0.45–0.80 km^2) compared to 1.13 km^2 (85% CI: 0.43–1.84 km^2) for high-exposure hens. The movement metric step length also did not differ between groups ($t = 2.23$, df = 10, $P \leq 0.246$). Mean 4-hour step lengths were 155.45 m (85% CI: 144.22–166.69 m) for low-exposure hens and 177.87 m (85% CI: 150.81–204.93 m) for high-exposure hens.

5.4.5 Movement linked habitat selection

In the iSSA models the only movement-related covariate that had support was cos_ta. In 27% of the models a negative cos_ta coefficient indicated that the movements of these individuals were characterized by turning back rather than having a forward directional persistence (Table 5.2). There did not seem to be any relationship between the importance of cos_ta and whether the individual was a high- or low-exposure female. The quadratic form of sagebrush cover and NDVI were the most consistent predictors of habitat selection. Sagebrush cover was important in 33% and NDVI was important in 50% of the individual models. Support for the quadratic form of sagebrush cover and NDVI suggests that females were showing a selection preference for intermediate values of these covariates and not extremely high or low values within their availability domain (Table 5.2 and Figure 5.4). The importance of NDVI was consistent across the high- or low-exposure groups while sagebrush cover was supported in 46% of the high-exposure and only 14% of the low-exposure individual models. The terrain roughness covariate (VRM) was supported in 22% of the individual models (Table 5.2 and Figure 5.4). The VRM coefficient was negative in all but one of these individual models suggesting brood-rearing females were consistently selecting for less rugged areas.

Grouse Id	**Cos_ta**	**VRM**	**Sage**	**Sage^2**	**NDVI**	**NDVI^2**
Low-exposure hens	***β*** **(85% CI)**	***β*** **(85% CI)**	***β*** **(85% CI)**	***β*** **(85% CI)**	***β*** **(85% CI)**	***β*** **(85% CI)**
HAR03	-0.196* (-0.348, -0.044)	0.054 (-0.043, 1.150)	0.179 (-0.573, 0.930)	-0.129 (-0.867, 0.609)	4.521* (1.705, 7.336)	-4.418* (-7.191, -1.646)
PAR11	0.011 (-0.125, 0.146)	0.040 (-0.066, 0.146)	0.121 (-0.318, 0.559)	-0.040 (-0.470, 0.390)	0.375 (-1.228, 1.977)	-0.728 (-2.347, 0.890)
PAR17	-0.078 (-0.215, 0.059)	-0.447* (-0.596, -0.297)	0.859* (0.386, 1.333)	-0.591* (-1.000, -0.181)	-0.077 (-1.389, 1.235)	0.011 (-1.286, 1.307)
PAR20	-0.139* (-0.274, -0.004)	0.036 (-0.079, 0.151)	-0.648 (-0.991, -0.304)	0.296 (-0.061, 0.653)	2.128* (0.927, 3.329)	-2.428* (-3.688, -1.168)
RAH06	-0.354* (-0.524, -0.184)	0.171* (0.042, 0.301)	0.494 (-0.056, 1.044)	-0.492 (-0.995, 0.011)	3.257* (1.112, 5.402)	-3.526* (-5.716, -1.336)
RAH15	0.168* (0.029, 0.308)	-0.075 (-0.197, 0.047)	-0.408* (-0.801, -0.016)	0.472* (0.121, 0.823)	-1.105 (-2.470, 0.260)	1.217 -0.103, 2.536)
RAH24	-0.095 (-0.228, 0.039)	0.007 (-0.092, 0.107)	-0.625* (-0.924, -0.325)	0.547* (0.257, 0.837)	-0.523 (-1.555, 0.508)	0.450 (-0.590, 1.490)
RAP03	-0.048 (-0.184, 0.087)	0.012 (-0.099, 0.123)	0.216 (-0.164, 0.596)	-0.176 (-0.521, 0.170)	2.314* (0.946, 3.683)	-2.083* (-3.412, -0.754)
RAP06	-0.261* (-0.433, -0.089)	-0.338* (-0.518, -0.159)	0.489 (-0.313, 1.292)	-0.516 (-1.301, 0.268)	-1.761* (-3.360, -0.161)	1.699* (0.116, 3.283)
RAP09	0.062 (-0.100, 0.224)	-0.071 (-0.210, 0.067)	0.796* (0.194, 1.397)	-0.840* (-1.425, -0.256)	-0.152 (-1.615, 1.310)	0.100 (-1.337, 1.538)
High-exposure hens						
HAR06	-0.047 (-0.212, 0.117)	0.032 (-0.085, 0.150)	0.682* (-0.032, 1.397)	-0.646* (-1.277, -0.015)	0.269 (-1.495, 2.032)	-0.181 (-1.898, 1.535)
HAR12	-0.314* (-0.475, -0.152)	-0.077 (-0.216, 0.063)	0.498 (-0.065, 1.061)	-0.309 (-0.181, 0.200)	0.186 (-1.802, 2.174)	-0.256 (-2.222, 1.710)
HAR17	0.017 (-0.160, 0.194)	-0.044 (-0.197, 0.109)	0.767 (0.133, 1.402)	-0.149 -0.667, 0.370)	-2.571* (-4.374, -0.768)	2.328* (0.607, 4.049)

PAR09	-0.004 (-0.137, 0.130)	-0.224* (-0.351, -0.097)	0.220 (-0.160, 0.601)	-0.175 (-0.537, 0.188)	0.774 (-0.857, 2.404)	-1.026 (-2.665, 0.612)
RAH08	-0.090 (-0.224, 0.044)	-0.014 (-0.117, 0.089)	0.127 (-0.209, 0.464)	-0.246 (-0.579, 0.088)	2.366* (0.900, 3.832)	-2.467* (-3.945, -0.989)
RAP19	-0.047 (-0.191, 0.098)	-0.310* (-0.466, -0.153)	1.537* (0.870, 2.205)	-1.144* (-1.705, -0.584)	-2.606* (-3.971, -1.241)	2.559* (1.267, 3.851)
RAP25	-0.216* (-0.393, -0.038)	0.053 (-0.088, 0.194)	0.518 (-0.009, 1.045)	-0.314 (-0.777, 0.149)	-0.872 (-2.513, 0.769)	0.722 (-0.879, 2.324)
RAP27	-0.089 (-0.223, 0.045)	-0.026 (-0.130, 0.077)	0.029 (-0.310, 0.368)	-0.197 (-0.531, 0.137)	3.852* (1.986, 5.719)	-3.902* (-5.781, -2.023)

Table 5.2: Beta coefficients for environmental and movement-related covariates that were significant (85% confidence interval [CI]) in our individual base models for brood-rearing female sage-grouse. Cos_ta explains the directional persistence of movements and was the only movement-related covariate that was significant in any of our individual models. Vector roughness measure (VRM) is a measure of terrain roughness. Sage + Sage^2 is the quadratic form of sagebrush cover. Normalized difference vegetation index (NDVI) is a measure of “greenness” or live green vegetation. NDVI + NDVI^2 is the quadratic form of NDVI. All covariates were modeled at a 30 x 30 m resolution. Cells shaded grey with an asterisk (*) by the coefficient indicate that the covariate was statistically supported (85% CI did not include zero).

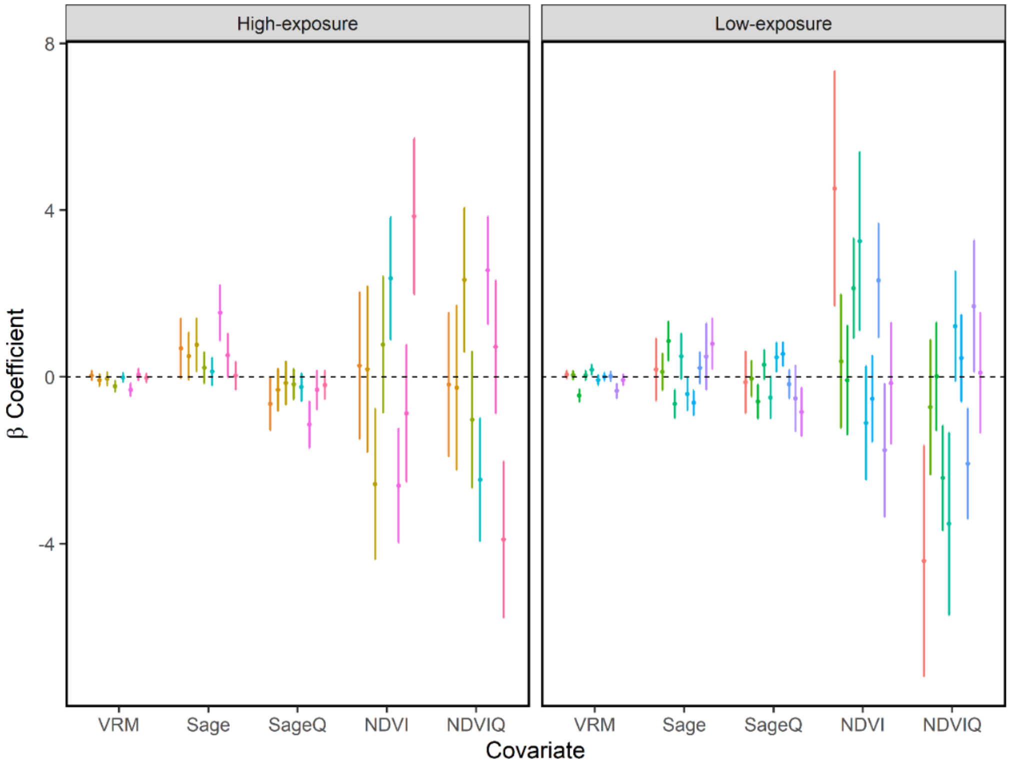


Figure 5.4: Beta coefficients and 85% confidence intervals (CI) for environmental covariates included in all individual models. Each color represents an individual (*n* = 18). The terms Sage + SageQ is the quadratic form of sagebrush cover and NDVI + NDVIQ is the quadratic form of NDVI. Covariates plotted for high- and low-exposure brood-rearing greater sage-grouse in northeastern Wyoming, USA.

Anthropogenic covariates were not explanatory and did not improve model fit in 28% of these individual models (Table 5.3 and 5.4). Eighty-three percent (*n* = 15) of the brood-rearing females were exposed to a surface disturbance covariate (Active disturbance, Reclamation or Landcover factor) within their availability domain (Table 5.3). Selection for natural landcover and against disturbed surfaces (active disturbance and reclamation) was the most commonly supported anthropogenic covariate in our individual models. Of the females exposed to anthropogenic disturbance, the Landcover factor was predictive in 33% of the individual models (Table 5.3). No individual models indicated a selection preference for disturbed surfaces (Table 5.3). Support for Landcover factor differed minimally between high-exposure (38%) and low-exposure females (29%) models (Figure 5.5). Continuous forms of active disturbance and reclamation covariates were supported in four models. The coefficient was generally negative suggesting that as active disturbance or reclamation increased within an area the likelihood of use decreased (Table 5.3). Only 39% of the brood-rearing females were exposed to reclamation, while 78% were exposed to active disturbance.

The majority (*n* = 16) of brood-rearing individuals were exposed to an anthropogenic feature covariate (Power line viewshed, Structure viewshed or Reservoir) within their availability domain (Table 5.4). Sixty-three percent of these individuals were exposed to power lines, either within their home range or adjacent to their home range, but within a 1.0 km viewshed distance (i.e., availability domain). A negative relationship between power line visibility and habitat use was detected in 30% (*n* = 3) of these models suggesting that areas with a greater number of visible power line poles were less likely to be used. Support for a negative relationship between power line visibility and habitat preference differed some between high (17%) and low exposure females (50%; Table 5.4).

We did not detect a consistent relationship between visible CBNG structures and habitat use (Table 5.4). Seventy-two percent of individuals were exposed to CBNG structures. All of these individuals, with the exception of one (*n* = 12), were only exposed to 3 m tall CBNG wells within their availability domain. A positive coefficient for the structure visibility covariates in two of the individual models suggested that these females were using areas with higher structure visibility values. One of these individuals (RAH06) had a positive coefficient for structure visibility but also showed strong avoidance of areas with more power line visibility (Table 5.4).

Experienced females were less likely than inexperienced females to establish home ranges in areas with anthropogenic disturbance or infrastructure features. Within their availability domain, 64% of experienced females were exposed to active disturbance, 45% were exposed to power lines (1.0 km viewshed distance of power lines) and 64% were exposed to CBNG structures (1.0 km viewshed distance of structures). In contrast, 100% of inexperienced females were exposed to active disturbance, 71% were exposed to power lines and 85% were exposed to CBNG structures (Figure 5.6). Experienced females were also more likely to demonstrate avoidance of areas with more power line visibility and higher percentages of active disturbance and no experienced females indicated a positive relationship with these covariates while two inexperienced females did (Figure 5.7).

Thirty-nine percent of brood-rearing females were exposed to reservoirs in their availability domain. Of these individuals, decay distance to reservoir edge was only supported in two models. In both cases, a negative coefficient suggested that as the distance from reservoir edge increased the likelihood of use also increased (Table 5.4). No individuals demonstrated a selection preference for areas adjacent to reservoirs.

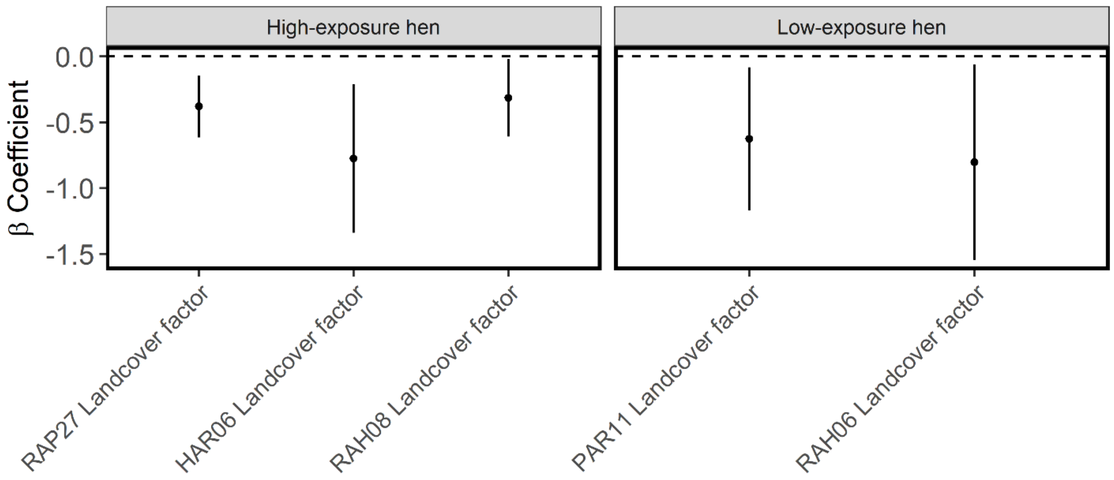


Figure 5.5: Beta coefficients and 85% confidence intervals (CI) for all individual models in which Landcover factor was supported. A negative coefficient for Landcover factor indicates selection for undisturbed natural vegetation (coded as 0) and against disturbed areas (coded as 1). Covariates plotted for high- and low-exposure brood-rearing greater sage-grouse in northeastern Wyoming, USA.

Table 5.3: Beta coefficients and 85% confidence intervals (CI) for anthropogenic surface disturbance covariates that were the most informative in our individual models for brood-rearing female sage-grouse. Active disturbances were areas stripped of natural vegetation (e.g., sagebrush shrubs) that remain devegetated or are partially vegetated with interim reclamation seed mixes. Reclamation were areas revegetated with reclamation seed mixes but largely devoid of sagebrush land cover. Active disturbance and reclamation covariates were quantified as the percent of disturbance per landscape pixel (0-100% active disturbance or reclamation). The Landcover factor covariate represented areas categorized into discrete classes of undisturbed natural vegetation or disturbed (active disturbance + reclamation). A negative coefficient for Landcover factor indicates selection for undisturbed natural vegetation (coded as 0) and against disturbed areas (coded as 1). All covariates were modeled at a 30 x 30 m resolution. An NA indicates that the individual was not exposed to that covariate. A dash (**—**) indicates that the individual was exposed to that covariate but the covariate was not statistically supported.

Grouse Id	**Active disturbance (%)**	**Reclamation (%)**	**Landcover factor (categorical)**
Low-exposure hens	***β* (85% CI)**	***β* (85% CI)**	***β* (85% CI)**
HAR03	NA	NA	NA
PAR11	—	NA	-0.626 (-1.169, -0.083)
PAR17	—	NA	—
PAR20	-0.254 (-0.401, -0.107)	NA	—
RAH06	—	NA	-0.803 (-1.546, -0.059)
RAH15	—	NA	—
RAH24	—	-0.187 (-0.354, -0.021)	—
RAP03	—	—	—
RAP06	NA	NA	NA
RAP09	NA	NA	NA
High-exposure hens			
HAR06	—	NA	-0.775 (-1.338, -0.211)
HAR12	—	NA	—
HAR17	—	—	—
PAR09	NA	—	—
RAH08	—	NA	-0.314 (-0.608, -0.020)
RAP19	—	—	—

RAP25	-0.285 (-0.521, -0.049)	–	–
RAP27	0.181 (0.080, 0.281)	–	-0.379 (-0.614, -0.144)

Table 5.4: Beta coefficients and 85% confidence intervals (CI) for anthropogenic infrastructure covariates that were the most informative in our individual models for brood-rearing female sage-grouse. Power line viewshed represented the number of power poles that were visible from any given pixel on the landscape. Structure viewshed represented the number of infrastructure features, such as coal-bed natural gas (CBNG) wells and compressor stations, that were visible from any given pixel on the landscape. We calculated how many power poles or structures were visible within a 1.0 km viewshed distance. These covariates were modeled at a 30 x 30 m resolution. Reservoir distance represents linear distances to man-made reservoirs transformed using a decay function ($e^{-d/\alpha}$) where 100 was a decay constant (α) and d was the distance in meters from each pixel to the reservoir edge which allowed the effect to decay as distance to the reservoir increased. An NA indicates that the individual was not exposed to that covariate. A dash (—) indicates that the individual was exposed to that covariate but the covariate was not statistically supported.

Grouse Id	**Power line viewshed (count)**	**Structure viewshed (count)**	**Reservoir distance (decay)**
Low-exposure hens	**β (85% CI)**	**β (85% CI)**	**β (85% CI)**
HAR03	NA	NA	NA
PAR11	NA	—	NA
PAR17	-0.338 (-0.538, -0.138)	—	—
PAR20	0.206 (0.097, 0.316)	NA	NA
RAH06	-0.661 (-1.128, -0.194)	0.364 (0.220, 0.509)	NA
RAH15	NA	—	NA
RAH24	NA	—	NA
RAP03	NA	0.188 (0.062, 0.315)	NA
RAP06	NA	NA	—
RAP09	—	NA	—
High-exposure hens			
HAR06	NA	—	NA
HAR12	—	—	-14.220 (-24.639, -3.809)
HAR17	—	—	—
PAR09	NA	NA	NA
RAH08	—	-0.202 (-0.321, -0.083)	NA
RAP19	-0.338 (-0.476, -0.199)	—	—

RAP25	–	–	-2.331 (-4.496, -0.165)
RAP27	–	–	NA

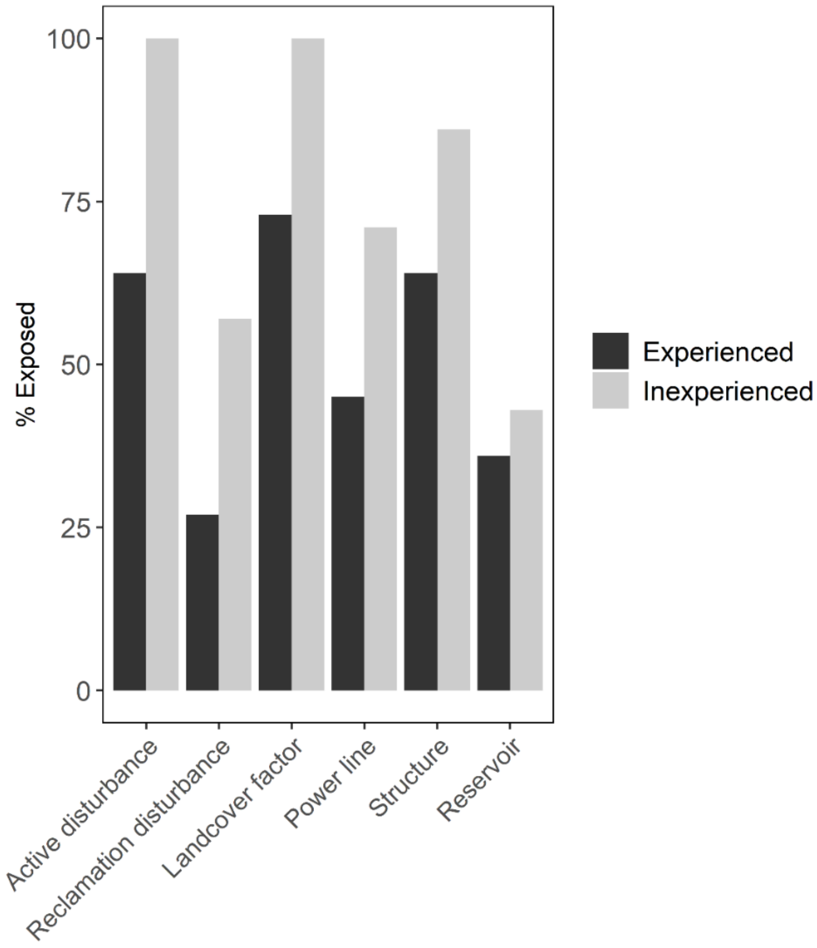


Figure 5.6: Comparison between the percent exposure of experienced (adult) and inexperienced (first year) brood-rearing greater sage-grouse to anthropogenic covariates within their availability domain in northeastern Wyoming, USA.

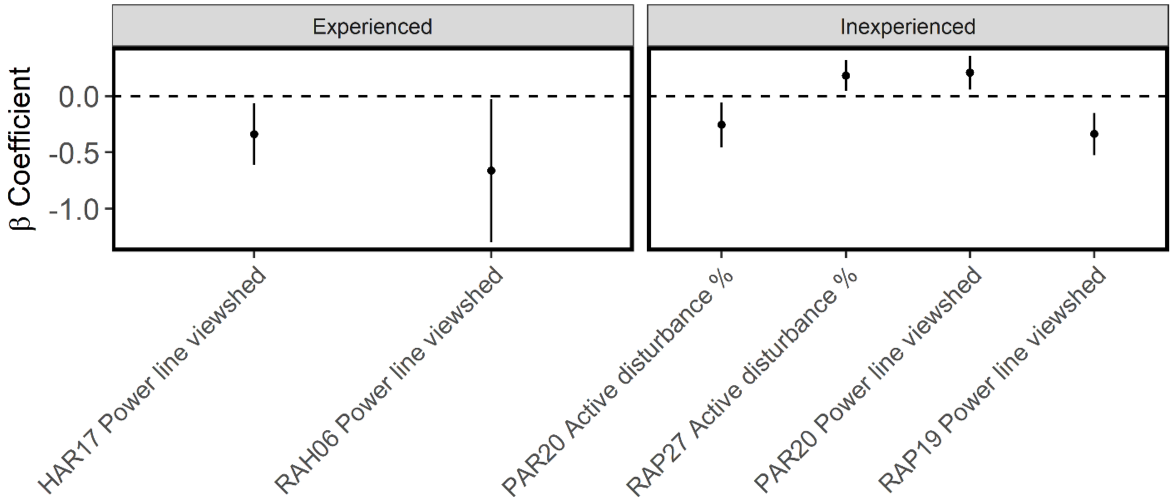


Figure 5.7: Beta coefficients and 85% confidence intervals (CI) for all individual models in which the covariates power line visibility and active disturbance were supported. Covariates plotted for experienced and inexperienced hens. Brood-rearing greater sage-grouse in northeastern Wyoming, USA.

5.5 Discussion

We evaluated several interrelated research questions using high-frequency relocation data from brood-rearing female sage-grouse in an energy development landscape. There was broad overlap between optimal brood-rearing habitat and CBNG development in our study area. Our findings reiterate the importance of contiguous sage-grouse habitat for brood-rearing females even if that habitat has been degraded by development. We did not find that individual differences in movements or home range sizes were explained by the amount of CBNG disturbance that brood-rearing females were exposed to at the level of the home range (high- and low-exposure females). Third-order habitat selection modeled at an individual-level reveled individual variability, but also consistent patterns of habitat selection and avoidance behaviors. Females consistently selected for natural landcover and avoided disturbed surfaces. Visible structures elicited different habitat selection responses. Power line visibility was generally negatively related to habitat selection, but visibility of shorter CBNG well structures did not seem to influence habitat selection. Our findings suggest that the age (adult or first year) of brood-rearing females explained some of the variability in home range (second-order) characteristics and third-order responses to development covariates.

5.5.1 Brood-rearing life stage

We assessed if the brood-rearing females in our study demonstrated distinct shifts in space-use patterns that would indicate two brood stages, early and late, between hatch and 40 days post-hatch. This step was necessary to accurately estimate home ranges and model third-order selection because others have suggested that hatch to about six weeks post-hatch could represent two distinct life stages (early and late brood-rearing; Atamian et al. 2010, Connelly et al. 2011*b*). Connelly et al. (2011*b*) suggested that early brood-rearing habitat is the habitat within the vicinity of the nest that is used by the brood-rearing females up to three weeks after hatching. We found no evidence supporting a two stage brood-rearing period or shifts in habitat use between 0-6 weeks after hatching. However, the majority of our brood-rearing home ranges were in close proximity or included the individual's nest site as described by Connelly et al. (2011*b*). This supports the hierarchical nature of the selection process by which female sage-grouse select nest sites (fourth-order) within larger areas (third- and second-order) that also provide resources needed to successfully raise chicks (Gibson et al. 2016). Our findings align with Hagen et al. (2007) that suggested female sage-grouse generally do not move from early to late brood-rearing habitats until after 6 weeks post-hatch; however, we did not evaluate brood-rearing female movements and space use after 6 weeks in this study. Furthermore, because our study population has been under energy development pressure for over a decade and is in a highly fragmented sagebrush landscape, we cannot rule out the possibility that the space-use patterns we observed were different from those that may have historically occurred in this population. Our results provide evidence that a temporally consistent pattern of early and late brood-rearing space use may not be uniform across the sage-grouse range and that a one-size-fits-all definition may not be prudent.

5.5.2 Home range, space use and movements

Contiguous sagebrush landcover is key to sage-grouse occupancy and survival at broad and fine spatial scales (Johnson et al. 2011*b*, Dinkins et al. 2014*b*, Fedy et al. 2014) and many studies have demonstrated that sage-grouse select for the flattest areas of sagebrush landcover available for nesting and brood-rearing (Fedy et al. 2015, Kirol et al. 2015*a*, Walker et al. 2016, Smith et al. 2018). Several of our brood-rearing home ranges were concentrated in the central portion of the study area. This area had more contiguous sagebrush landcover and gentler topography than the surrounding landscape (Figure 5.1). The central portion of our study area also contained the highest density of CBNG infrastructure. Energy development often targets areas of flatter terrain because development costs increase with topographic ruggedness (Walker et al. 2020). Walker et al. (2020) observed a similar energy development pattern in Colorado, USA where areas of sagebrush landcover with gentler topography, that also had disproportionately high sage-grouse use, were the areas experiencing the most development pressure (Walker et al. 2020). The overlap between energy disturbances and optimal nesting and brood-rearing habitat may be even more pronounced in our study area because it is characterized by rugged terrain and a patchy distribution of sagebrush landcover compared to much of the sage-grouse range (Fedy et al. 2014, 2015).

As expected, females in our study established brood-rearing home ranges in areas that were dominated by sagebrush landcover. The proportion of sagebrush landcover within individual home ranges averaged 77% and no individuals established home ranges in areas with less than 40% sagebrush landcover. The proportion of sagebrush landcover in our brood-rearing home ranges reiterates that, while access to food resources like insects and forbs are critical to chick production (Blomberg et al. 2013*a*), these resources need to be available in conjunction with adequate sagebrush cover (Cassaza et al. 2011, Connelly et al. 2011*b*, Smith et al. 2018).

Brood-rearing sage-grouse in our study established home ranges in areas that had 3.5% anthropogenic surface disturbance on average. This estimate included both active disturbance and reclamation. Kirol et al. (2020*a*) showed that during the reproductive life stages female sage-grouse, from multiple regions in Wyoming, USA, consistently occupied areas with less surface disturbance relative to what was available to them. Ninety percent of nesting and brood-rearing locations were in areas with < 3% disturbance within a ~3-km^2 area (Kirol et al. 2020*a*). Researchers have pointed to similar percentages of surface disturbance when studying impacts of energy disturbance on other sagebrush associated species. For instance, the presence and abundance of the pygmy rabbit (*Brachylagus idahoensis*) declined sharply once oil and gas surface disturbance reached 2% and mule deer (*Odocoileus hemionus*) rarely used areas with greater than 3% oil and gas disturbance during migration (Germaine et al. 2017, Sawyer et al. 2020).

We tested the hypothesis that brood-rearing females exposed to higher percentages of anthropogenic surface disturbance (high-exposure females) would demonstrate different movement and space-use patterns than those exposed to less disturbance (low-exposure females). Because sage-grouse with chicks are particularly sensitive to energy development (Aldridge and Boyce 2007, Kirol et al. 2015*a*), we suspected that females in areas with more disturbance would restrict their movements to avoid anthropogenic edge, such as graveled CBNG access roads and structures, such as power lines. For instance, research has demonstrated that power line corridors constrain movements of prairie-chickens (*Tympanuchus* spp. Pruett et al. 2009). We expected that restricted movements in highly disturbed areas would lead to smaller home ranges. However, we did not detect a difference in movements or home range sizes between low-exposure and high-exposure females. However, the distribution of energy development covariates were limited in two important ways in our study. First, almost all of our birds were exposed to energy development and therefore we did not have birds that raised their broods in a 'control' or unimpacted area. Ideally, to maximize our potential to detect a biological difference, we would compare brood-rearing females that were not exposed to any disturbance to females exposed to high percentages of disturbance.

5.5.3 Movement linked habitat selection

The movement related covariate (cos_ta) was supported in about 39% of our iSSA individual models. In all but one of these models a negative coefficient indicted that the female was generally turning back rather than moving forward. This is consistent with home range behavior in that females in our study had core areas within their home ranges and were generally turning back towards those core areas. When animals are migrating or dispersing this movement covariate (cos_ta) is consistently positive suggesting a forward-directional persistence (Prokopenko et al. 2017).

Many studies have documented the importance of sagebrush cover for brood-rearing sage-grouse (Cassaza et al. 2011); yet, sagebrush cover was only informative in one third of individual models. In the context of a hierarchal selection process, the minimal support for the sagebrush cover covariate in our third-order models was not surprising because iSSA models bound availability to what is available to that individual at that time. Since females in our study established home ranges (second-order) in areas that were dominated by sagebrush landcover the availability domains for the iSSA models were constrained to within areas of sagebrush cover. In the cases when sagebrush cover was informative, females were selecting for patches (900-m^2 area) of intermediate levels of sagebrush canopy cover. This selection for intermediate levels of sagebrush cover and not for the high and low cover extremes is consistent with previous research (Aldridge and Boyce 2007, Doherty et al. 2010, Kirol et al. 2015*a*).

Third-order selection for natural landcover (Landcover factor) and against disturbed surfaces (i.e., active or reclamation surfaces) was consistent across 33% percent of the females and no females showed a preference for disturbed surfaces. This finding concurs with much research demonstrating that females with chicks are highly reliant on natural sagebrush vegetation communities (Connelly et al. 2011*b*) and at local scales (third- and fourth-order), brood-rearing females select for structure, cover and food (Smith et al. 2018). In response to perceived risks related to human activity (e.g., vehicle traffic or industrial noise; Frid and Dill 2002, Blickley et al. 2011), we predicted that natural vegetation in combination with sagebrush cover might be more important to high-exposure than low-exposure females because these vegetation attributes provide refuge habitat for females and chicks and were generally more limited in areas with more surface disturbance. However, our results suggested there was similar support for sagebrush cover and natural vegetation covariates in our high-exposure and low-exposure female models.

Our findings did not provide evidence that brood-rearing females were treating reclamation surfaces differently than active surfaces. However, only 39% of brood-rearing females in our study were exposed to reclaimed surfaces so our sample size was limited. The proportion of reclamation per area was only informative in one individual model and this female was selecting against areas (900 m^2) with more reclamation surface. It can take big sagebrush >80 years to naturally reestablish on disturbed surfaces (Avirmed et al. 2015). Therefore, the reclaimed surfaces in our study represent early-stage reclamation (≤10 years since the surface was reclaimed). Pipeline corridors were the primary reclamation surface within our brood-rearing home ranges and these reclaimed surfaces were often in close proximity to active development making it difficult to tease out effects of reclamation on habitat-selection patterns of female sage-grouse. More research is needed to better understand the relationship between reclaimed surfaces and sage-grouse habitat selection, especially in areas where entire landscapes have been reclaimed and the human activity component of energy disturbance has subsided (sensu Barlow et al. 2020).

Visible structures were not universally related to avoidance behavior in our study. We found greater power line visibility often elicited an avoidance response in brood-rearing females, but visible CBNG well structures generally did not. Thirty percent of the individuals exposed to power lines were less likely to use areas with greater power line visibility and as the amount of power lines visible from an area increased the probability of selection of that area decreased. Dinkins et al. (2014*b*) found the density of power lines within a 1-km^2 area was negatively related to female sage-grouse survival. They concluded that reduced survival was likely a consequence of power lines acting as perching structures for raptors (Dinkins et al. 2014*b*). Others have shown that power lines also provide perching structures for common ravens (*Corvus corax*) that depredate sage-grouse nests and chicks (Hagen 2011, Coates et al. 2014, Gibson et al. 2018). Several species of raptors were common in our study area (sensu Tack and Fedy 2015). Common ravens were uncommon during our study but ravens are currently expanding into this region (Kirol et al. 2015*b*, *unpublished data*). Brood-rearing females in our study may have recognized the increased risk of using habitats near power lines. In our study we demonstrated that brood-rearing sage-grouse avoid areas ≤1 km from power line corridors. Therefore, the ecological footprint was much larger than the actual disturbance footprint of power lines because of the functional habitat loss due to avoidance behavior. Previous studies have shown sage-grouse avoid otherwise suitable habitat when power lines are introduced and this avoidance can sometimes extend 4 km from power line corridors

(Dinkins et al. 2014*b*, Lebeau et al. 2019). The avoidance of power lines may be common in prairie grouse (Pruett et al. 2009, Hovick et al. 2014).

CBNG wells in our study area were generally small buildings (~2x2 m structure) and approximately two meters tall with instruments that rose another one meter above the building. Thus, they were much shorter than power lines (~24 m) and provided limited perching opportunities. Our inference about taller CBNG infrastructure, such as compressor or pumping stations (5-8 m tall), was limited because female home ranges were rarely within 1 km (viewshed distance) of these structures and only one female had a compressor or pumping station within her home range and it was only slightly within her home range (i.e., outside the 98% isopleth). While 72% of our brood-rearing females were within a 1 km viewshed distance of CBNG wells, our results suggested there was no relationship between well visibility and habitat selection for the majority of the individual models and two individuals showed a positive relationship between CBNG well visibility and habitat selection. Collectively, these results suggest that visibility of CBNG wells were not predictive of third-order selection of brood-rearing females. This finding is in contrast to Kirol et al. (2015*a*) that found the likelihood of an area being used by brood-rearing females declined as the number of visible CBNG wells increased.

An important consideration is the stage of energy development in our study (production phase). When we began putting transmitters on birds, the CBNG infrastructure had been in place for >10 years. Because of a reduction in traffic, heavy machinery (e.g., drilling rigs), industrial noise and human presence, the environment experienced by the animals is much different during the production phase than during the development phase (Ingelfinger and Anderson 2004, Sawyer et al. 2009, Holloran et al. 2015). Like the majority of wildlife impact studies, the Kirol et al. (2015*a*) study was conducted when an area was first being developed for CBNG reserves (development phase). We suspect that the avoidance of visible CBNG wells identified by Kirol et al. (2015*a*) may have more to do with the human activity associated with those wells than the ~3 m tall structure. Therefore, the different phase of development between this study and our current study may partially explain the differences observed in avoidance behavior of brood-rearing females. Prey have evolved antipredator behavioral responses to perceived threats, such as loud noises and rapidly approaching objects (Frid and Dill. 2002). Vehicles can lead to antipredator responses in many animals and avoidance behavior is an example of an antipredator response (Frid and Dill 2002, Lyon and Anderson 2003). Studies have demonstrated that sage-grouse and other bird species respond negatively to vehicle traffic in energy development landscapes; however, these negative responses may be reduced with lower traffic volumes (Lyon and Anderson 2003, Ingelfinger and Anderson 2004, Holloran 2005). During the production phase of energy development vehicle traffic can be as high as 75 vehicles per hour (Ingelfinger and Anderson 2004). Sawyer et al. (2009) recorded 112 vehicles passing per day accessing well pads that were being drilled in a natural gas field in southern, Wyoming, USA. During our study, vehicle traffic recorded on a main haul road ─ main road that branched off into multiple well access roads ─ that bisected one of our brood-rearing home ranges averaged 21 vehicles passing per day during the brood-rearing period (*unpublished data*).

We were able to quantify patterns of variability across age classes in the response of female sage-grouse to energy development that would not have been apparent if we were pooling all individuals in population-level models. For instance, while selecting brood-rearing habitat the only females that did not avoid areas with greater power line visibility or higher percentages of active disturbance were first year females. At the level of the home range (second-order), first year females were also more likely than adult females to be exposed to CBNG features including power lines, well structures and man-made reservoirs, because they were more likely to establish home ranges in areas with anthropogenic disturbance. Other research has shown that an animals age and experience can influence habitat selection and space use. Cresswell (1994) showed that juvenile redshank (*Tringa tetanus*) primarily feed on saltmarshes while adults primarily feed on mussel beds. The saltmarshes were riskier habitats and; consequently, juvenile redshanks experienced more predation than the adults. Based on previous experiences, birds will modify their habitat-selection patterns to avoid predation of themselves, nests, or dependent young (Lima 2009). Therefore, it is possible that inexperienced female sage-grouse do not recognize the risk associated with brood-rearing in areas with more power lines and more anthropogenic habitat fragmentation, while experienced females have learned that these areas are riskier.

5.5.4 Conclusions

Optimal brood-rearing habitat is limited for female sage-grouse in our study area and the optimal habitats contained a high density of energy disturbance. Within these development landscapes females established home ranges in areas that contain more contiguous sagebrush landcover and fewer CBNG features.

Individual-level selection analyses conducted at the third-order helped us uncouple some aspects of energy development that influence habitat selection that likely would not have been detected at broad spatial scales (e.g., second-order). For instance, female brood-rearing sage-grouse did not respond the same to all structures. Power lines generally lead to avoidance behavior; however, 3 m tall CBNG wells did not. Even though most of the brood-rearing females were in close proximity to active and reclamation surface disturbance within their home ranges, they selected for natural vegetation and avoided disturbed surfaces at fine spatial scales. As a whole there was more individual variability in our third-order habitat selection models than expected. Therefore, our results do not support individual uniformity in brood-rearing sage-grouse. We found that first year females were more likely than adults to not demonstrate avoidance at the third-order of selection and were also more likely to establish home ranges in areas with CBNG features. We suggest that individual variation between adults and first year females may be explained by the previous experience of the landscape by the adults leading to selection for less risky habitats. However, more research is needed to better understand drivers of individual variation in female sage-grouse. It is not feasible for management and conservation to occur at an individual level; however, we demonstrate that it is important to understand there is variation in individual sage-grouse within populations. Furthermore, these findings reiterate the importance of accounting for, or at least recognizing, individual variability in population-level modeling efforts (Duchesne et al. 2010).

Chapter 6

Discussion

Our research represented management-oriented science related to the conservation of sagebrush associated species. We used a sagebrush-obligate songbird, the Brewer's sparrow (*Spizella breweri breweri*), and the greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) to address question related to habitat selection, space use, reproductive rates and movements in an established coal-bed natural gas (CBNG) field. This CBNG field was developed over a decade ago and during our study some wells were at the end of their production life and undergoing site reclamation. Most studies of wildlife and energy development impacts are conducted when the development is first occurring and, thus is novel to the co-occurring species. However, the birds in our study represented multiple generations that have been exposed to CBNG development. We uncoupled the components of CBNG development into specific infrastructure features and surface disturbance covariates, such as active disturbance and reclamation, to gain a better understanding of responses of these species to the different components of energy development (e.g., power lines or CBNG well structures) and site reclamation. The individual-based models we used in our sage-grouse analysis helped us better understand individual variability in responses to CBNG features. We suggested that individual variability we observed was partially explained by the age and experience of the female sage-grouse. We hope this information will help focus mitigation efforts on the components of energy development that have the greatest negative impacts on sagebrush-obligate birds.

6.1 Sage-grouse tracking and capturing advances

Our research objective required capturing female sage-grouse to attach GPS transmitters (i.e., tags). In Chapter 2, we describe a method of capturing sage-grouse that proved to be effective in our study area, that contains a low density of sage-grouse, and minimized capturing impacts when compared to other commonly used capturing techniques.

The sage-grouse tag (hybrid tag) and harness we describe in Chapter 3 was designed to be cost-effective and to reduce impacts of fitting rump-mounted tags on sage-grouse while also providing the high-resolution GPS location data that we needed to address our research questions. Research that requires tracking animals, needs to be able to securely attach tags in a way that does not harm the animal or affect the animal's behavior (Barron et al. 2010). Fitting tags on birds may have deleterious effects depending on a variety of factors such as the attachment method and the proportionate mass of the tag (Barron et al. 2010, Fair et al. 2010). However, there is a general consensus that potential detrimental effects of tags fitted on birds are reduced with proportionally lighter tags (Fair et al. 2010, Vandenabeele et al. 2012). Necklace-style (hereafter necklace) very-high frequency (VHF) tags have been used on sage-grouse and other Galliformes for decades and there is abundant information on possible effects of these tags on behavior and survival. Of note, early research suggested not using necklace tags on male sage-grouse because of interference with the air sacs used in lekking displays (Amstrup 1980); therefore, my comparisons below only reference research of female sage-grouse fitted with necklace tags. Rump-mounted solar tags are a fairly new tracking method used in sage-grouse research (Bedrosian and Craighead 2010) and there is little information available on how these type of tags may affect sage-grouse behavior and survival.

Like all species of Galliformes, sage-grouse are targeted by a variety of raptor and mammalian predators and predation is the leading cause of adult mortality usually accounting for greater than 90% of deaths (Blomberg et al. 2013*b*). Therefore, research focused on potential impacts of tags on sage-grouse survival are really trying to understand if individuals fitted with tags are at higher predation risk than those that are not fitted with tags (Frye et al. 2014). It is difficult to uncouple 'natural' survival rates in sage-grouse from survival rates of tagged sage-grouse because of the challenges in collecting the data necessary to estimate survival rates when birds are not tagged. However, there is some research available on annual survival that used leg band recovery data (Zablan et al. 2003). The annual survival rates they report are very similar to survival estimates reported by numerous studies that used necklace tags on female sage-grouse (Schroeder et al. 1999, Zablan et al. 2003, Connelly et al. 2011*a*). Hagen et al. (2006) studied another gallinaceous bird, the lesser prairie-chickens (*Tympanuchus pallidicinctus*), found that survival estimates of birds fitted with necklace tags were not different than non-tagged birds that were banded. Research on flushing behavior in sage-grouse found no difference in flushing order (flushing earlier or later than flock mates) between necklace tagged and non-tagged birds (Frye et al. 2014). The large amount of information available on necklace tags used in sage-grouse research suggests that these type of tags do not contribute to increase predation risk or significantly alter sage-grouse behavior.

However, there is much less information available on potential effects of rump-mounted tags on survival and behavior of sage-grouse and other Galliformes. This can be attributed to the fact that solar GPS units light enough to attach to gallinaceous birds are a recently developed technology (Bridge et al. 2011). Studies that we are aware of that have evaluated potential impacts of rump-mounted tags on sage-grouse were all using Argos satellite relay tags (hereafter Argos tags). The hybrid tags we attached to female sage-grouse in our research were similar to the Argos tags in many ways and both are attached to birds using a rump-mounted harness system. However, the hybrid tag we developed was slightly lighter

(≤4 g; lower tag-to-body mass ratio) than Argos tags, commonly used in female sage-grouse studies, and the hybrid tag did not have a ridged antenna protruding from the back of the unit as do Argos tags (Severson et al. 2019).

Some of the earliest research that used rump-mounted Argos tags on sage-grouse found that sage-grouse fitted with rump-mounted tags did not experience increased mortality when compared to sage-grouse fitted with conventional necklace tags (Bedrosian and Craighead 2010). Bedrosian and Craighead (2010) concluded that rump-mounted tags had minimal impacts on sage-grouse in their study. Foster et al. (2018) suggest that sage-grouse with rump-mounted tags may have had slightly reduced survival (~5%) compared to those with necklace tags but the results were inconclusive because of marginal statistical support. A recent study conducted by Severson et al. (2019) found that female sage-grouse fitted with necklace tags had median survival estimates that were 1.08 to 1.19 times greater than those fitted with rump-mounted Argos tags. Their results also suggested that proportionally heavier (tag-to-body mass ratio) rump-mounted tags lead to lower survival (Severson et al. 2019).

Further studies are needed to gain a better understanding of potential effects of attaching rump-mounted tags to sage-grouse. This information is critical to help researchers weigh the cost and benefits of fitting sage-grouse with rump-mounted tags, especially in areas where sage-grouse numbers are low.

6.2 Brewer's sparrow

6.2.1 Caveats, research considerations and future research

Survival analyses are particularly sensitive to sample sizes and, more importantly, the numbers of events of interest), such as nest failure in our study (Concato et al. 1995, Hosmer and Lemshow 2008). More events per explanatory covariate increase the power of the analysis to detect influential covariates and improve the precision of estimates and error terms (Concato et al. 1995, Hosmer and Lemshow 2008). Our Brewer's sparrow nest survival analysis (Chapter 4) had a robust sample size broadly (n = 107 nests, n = 50 events [nest failures]) but sample sizes and corresponding events were more limited when we modeled specific anthropogenic covariates of interest, like the proportion of active disturbance per scale. For instance, we found a relationship between the proportion of active disturbance within 50 m radius of a Brewer's sparrow nest site and nest survival. Yet, this relationship was only informed by ten events (n = 23 nests). Therefore, a larger sample size of nests that were associated with the anthropogenic covariates of interest in this research (e.g., active disturbance, reclamation and power lines) would have benefited our survival modeling and resulted in greater precision in our estimates and error terms (i.e., tighter confidence intervals). The distribution of nest sites in our study suggest that Brewer's sparrows were, on average, avoiding placing nests in areas with higher proportion of habitat disturbance which acted to limit our sample sizes in regards to the anthropogenic covariates of interest. However, we may have been able to increase sample size of nests relative to disturbance covariates if we targeted additional areas that were proximate to active disturbance, reclamation and power lines when nest searching.

Nest productivity is a critical component of population persistence in birds and nest predation is the primary cause of nest failure (Saether and Bakke 2000, Chalfoun et al. 2002, Ibáñez-Álamo et al. 2015). Our work in Chapter 4 and other research demonstrate that anthropogenic development and habitat fragmentation may lead to co-occurring songbird nests being at increased risk of predation (Winter et al. 2000, DeGregorio et al. 2014, Hethcoat and Chalfoun 2015*b*, Bernath-Plaisted and Koper 2016). In disturbed sagebrush habitats, there is limited information on the nest predator component that are responsible for these lower nest survival rates (Sanders and Chalfoun 2019). More research is needed that focuses on nest predators in sagebrush habitats to gain a more mechanistic understanding of why nest predators are more likely to locate and depredate bird nests in association with anthropogenic disturbance. Changes in nest survival might be explained by different predator communities and predator abundance in disturbed habitats (Hethcoat and Chalfoun 2015*b*) or the expansion of novel predators that may be benefiting from human subsidies (Howe et al. 2014, Kirol et al. 2018). Reduced nest survival could also be explained by native predators gaining a competitive advantage in sagebrush habitats that have been fragmented by anthropogenic development which has been demonstrated in forest and grassland ecosystems (Winter et al. 2000, Chalfoun et al. 2002, Vander Haegen 2007).

Reclamation surfaces in our study, represented early-stage reclamation; therefore, the primary difference between disturbances that had been reclaimed and those that had not been reclaimed was that reclaimed surfaces no longer had the CBNG infrastructure and, instead of gravel roads or compacted surface well pads, contained seeded grass and forb ground cover. Our findings in Chapter 4 suggest that Brewer’s sparrow nest survival is lower when nests are exposed to higher levels of active disturbance but when nests are exposed to comparable proportions of reclamation there was no effect on nest survival. This finding suggests that the removal of infrastructure and the human activity component (e.g., vehicle traffic to monitor wells) changed the relationship to nest survival. Therefore, another important avenue of research is how nest predator communities respond to reclamation and infrastructure removal. Specifically addressing the question, if some nest predators are benefiting from human subsidies, such as perching structures, do they lose their competitive advantage if these structures are removed?

Sage-grouse are often considered an umbrella species for other sagebrush dependent wildlife (Rowland et al. 2006, Hanser and Knick 2011). The umbrella species concept assumes that protection of one species provides benefits to other naturally co-occurring species (Roberge and Angelstam 2004). With sage-grouse, the assumption is that by conserving sage-grouse habitat you are also benefiting other sagebrush associated species under its umbrella (Hanser and Knick 2011). For the umbrella species concept to be effectively applied, habitat requirement of species under the sage-grouse umbrella need to be well understood (Hanser and Knick 2011, Barlow et al. 2019). The umbrella species concept, like habitat selection, is scale dependent. For instance, the sage-grouse has been shown to be an effective umbrella for sagebrush associated songbirds at broad spatial scales (first- and second-order selection; Hanser and Knick 2011, Carlisle et al. 2018*b*) but much less is known about its effectiveness local scales (third- and fourth-order; Barlow et al. 2019). Barlow et al. (2019) found that Brewer's sparrows and sage-grouse select for some similar habitat attributes at the nest site but also some different attributes. They conclude that, fine-scale habitat management for sage-grouse as a proxy for conservation of other species may be justified if the microhabitat preferences of the species under the umbrella are understood to avoid unintentional negative effects (Barlow et al. 2019). More research is needed to understand fine-scale habitat preferences and habitat partitioning of bird species that nest in sagebrush habitats and that fall under the sage-grouse umbrella. For example, we observed a large diversity of nesting birds within relatively small sagebrush patches in our study area. In our 0.25 km^2 nest searching plots (Chapter 4) across the three years of our study (2016-2018), we discovered nest of Brewer's sparrow, Brewer's blackbird (*Euphagus cyanocephalus*), common nighthawk (*Chordeiles minor*), sage-grouse, short-eared owl (*Asio flammeus*), lark bunting (*Calamospiza melanocorys*), lark sparrow (*Chondestes grammacus*), loggerhead shrike (*Lanius ludovicianus*), mallard (*Anas platyrhynchos*), mourning dove (*Zenaida macroura*), sage thrasher (*Calamospiza melanocorys*), spotted towhee (*Pipilo maculatus*), vesper sparrow (*Anas platyrhynchos*) and western meadowlark (*Sturnella neglecta*; *unpublished data*).

6.3 Sage-grouse

6.3.1 Caveats, research considerations and future research

In Chapter 5, we modeled third-order selection of female sage-grouse during the brood-rearing life stage because the ability of females to successfully raise chicks to independence is critical to sage-grouse population persistence and research has demonstrated that brood-rearing females are particularly sensitive to energy development (Aldridge and Boyce 2007, Kirol et al. 2015*a*). By using the integrated step selection analysis (iSSA) we were able to assess third-order selection of individuals while simultaneously accounting for the movement process. However, because the majority of females in our study were fairly localized during the brood-rearing period and, on average, not moving far (e.g., short step lengths) the iSSA analysis had less power to identify movement relationships relative to environmental and anthropogenic covariates. When animals are moving they are more likely to move through a greater diversity of landcover types and encounter a variety of anthropogenic features and disturbances. The ideal application of iSSA is when animals are moving or dispersing because one is able to learn more about the environmental and anthropogenic factors that are affecting the movement process. For example, Scrafford et al. (2018), using iSSA, found that wolverines (*Gulo gulo luscus*) increased their movements near roads and their movements increased even more when they encountered higher traffic roads. Dickie et al. (2019) found that moose (*Alces alces*), black bear (*Ursus americanus*) and wolf (*Canus lupus*) exhibited the slowest movements when they were traveling through undisturbed habitats and fastest movements when traveling in areas with anthropogenic linear features such as seismic lines and roads. Applying the iSSA model to a life stage when sage-grouse are dispersing like when they are transitioning to winter range (Fedy et al. 2012) would likely allow for more insight into anthropogenic and environmental factors that are affecting the movement process in sage-grouse.

Comparisons to previous studies of impacts of energy development on sage-grouse suggest that brood-rearing sage-grouse in this population may be exhibiting less avoidance behavior towards infrastructure features, notably well structures (Holloran et al. 2010, Kirol et al. 2015*a*). In Chapter 5, we hypothesize that the phase of development (e.g., development or production phase) may partially explain the reduced avoidance of visible CBNG well structures we observed when compared to other studies that were conducted when the development was first occurring (i.e., more human activity and greater traffic volumes during the development phase). However, there may be more than one factor at work here. For instance, there could be less avoidance due to lower levels of human activity during the production phase as well as a degree of habituation that might be occurring in our study population.

The sage-grouse population we studied had been exposed to energy development for >10 years when this study was initiated. Therefore, female sage-grouse in our study represent multiple generations that have nested or raised chicks in this development landscape. Therefore, the idea that there may be a level of habituation occurring is a possibility that warrants further research. In the context of anthropogenic development, habituation assumes that negative behavioral responses exhibited by animals (e.g., avoidance behavior) towards novel features, such as oil and gas wells, may gradually dissipate over time (Blumstein 2016, Sawyer et al. 2017). It is important to note, however, that habituation does not imply population fitness because human-altered landscapes can lead to lower reproductive rates and may act as ecological traps for many animals including sage-grouse (Robertson and Hutto 2006, Aldridge and Boyce 2007, Kirol et al. 2020*a*).

In Chapter 5, we quantified landcover and surface disturbance (i.e., active and reclaimed disturbances that quantified the direct loss of natural vegetation) within brood-rearing home ranges. The distribution of the home ranges in our study and our findings related to landcover and surface disturbance within these home ranges lead to questions about selection occurring at broader spatial scales. The logical next step in our research is to evaluate selection at the home range level (i.e., second-order selection) during the brood-rearing life stage to better understand brood-rearing female tolerance related to surface disturbance and infrastructure features at a higher order of selection (Holbrook et al. 2017). For instance, even though there were compressor stations distributed throughout the study area we only had one brood-rearing female that had a compressor station within her home range and the compressor station was only slightly within her home range (i.e., outside the 98% isopleth). A second-order analysis should help us understand if this was random or if brood-rearing females were actively avoiding compressor stations when establishing home ranges.

Federal and state management agencies are increasingly focusing on surface disturbance caps to regulate disturbance within the sagebrush ecosystem and to mitigate impacts on sage-grouse and other sagebrush associated wildlife. For example, the Wyoming Core Area policy caps surface disturbance to 5% when development projects occur within Core Areas. Core Areas are areas previously identified as containing high sage-grouse breeding population densities (Doherty et al. 2011). However, not all areas identified as sage-grouse core population areas by Doherty et al. (2011) were included as Core Areas in the state and federal management plans (BLM 2015, State of Wyoming 2019, Kirol et al. 2020*a*). The south central portion of our study area contained the majority of brood-rearing home ranges. This area is an example of an area identified through science as a sage-grouse population core area that was not included as a Core Area in the Core Area policy (Doherty et al. 2011, BLM 2015, State of Wyoming 2019). Therefore, this area provides a unique opportunity to evaluate possible thresholds of tolerance of brood-rearing females to varying levels of surface disturbance. In Chapter 5, we found that the proportion of surface disturbance averaged 3.59% across individual home ranges. Research using peak male sage-grouse lek counts as a population index, demonstrated that surface disturbance >3% led to local sage-grouse population declines (Knick et al. 2013). Through previous research that occurred in this same region we know that of surface disturbance levels exceed 3.59% in much of our study area (Kirol et al. 2020*a*); therefore, female sage-grouse with chicks may, on average, be selecting home ranges in patches of sagebrush with lower levels of disturbance relative to what is available to them. A second-order selection analysis would help us understand if selection for home ranges with lower proportions of disturbance is occurring and identify the remaining lower disturbance sagebrush areas that are suitable brood-rearing habitats.

In our analysis we separated disturbance into active disturbances and reclamation. Active disturbances were areas stripped of vegetation that remain devegetated or are partially vegetated with interim reclamation seed mixes such as graveled access roads and well pads (Figure A3). Reclamation included areas without above ground infrastructure that had been revegetated with reclamation seed mixes but were largely devoid of sagebrush (Figure A4). One brood-rearing female in our study established a home range in an area that had a level of surface disturbance (14.65%) that was almost four times as high as the average surface disturbance across all individuals (3.59%). A large portion of surface disturbance within this individual's home range was reclamation (5.33%). This female was an outlier but raises questions about tolerance levels related to different types of surface disturbance. That is, would this female have established a home range in this area if all of this disturbance was active disturbance? A second-order selection analysis would allow for greater inference into possible differences in responses to reclaimed versus active disturbances (Holbrook et al. 2017). In our third-order selection analysis (Chapter 5), we did not find evidence that female sage-grouse were responding differently to active disturbances and reclamation surfaces during the brood-rearing period. However, at broader spatial scales (i.e., second-order) we may observe different responses to reclamation and active disturbance.

Animal occurrence considered alone can be a misleading indicator of population fitness in human-altered landscapes (Van Horne 1983, Robertson and Hutto 2006). Research is needed in northeastern Wyoming that seeks to identify source habitats that are creating a surplus of individuals before these areas are degraded further by energy development or other anthropogenic disturbances (Pulliam and Danielson 1991, Kirol et al. 2015*a*). This information is need to focus conservation efforts on these sage-grouse nurseries that are critical to the persistence of sage-grouse in this region.

6.1 Final remarks

Given the continued energy development pressures on the sagebrush ecosystem, developing best management practices and using adaptive management approaches that are based on science will be essential to maintain wildlife species that are dependent on sagebrush habitat (Boyce et al. 2011, Naugle et al. 2011, Nichols et al. 2015). Our study helped advance capturing and tracking technologies that are transferable to a variety of other bird species and research. Our study filled in knowledge gaps related to the response of sagebrush nesting birds to post-development reclamation and active energy development.

Our individual-level models helped us better understand sage-grouse habitat selection, space use, movements in an established natural gas field and during a critical reproductive life stage for sage-grouse.

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Appendix A

Photographs of coal-bed natural gas (CBNG) disturbance in northeastern Wyoming, USA

Figure A1. Reclaimed access road.

Figure A2. Reclaimed well pad.

Figure A3. CBNG infrastructure with a well and access road in foreground and a compressor station in the background.

Figure A4. Reclaimed surface, pipeline corridor.

Figure A5. CBNG well and pad.

Figure A6. Compressor station.

Figure A7. Power lines.