

GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) NEST SURVIVAL AND
NEST PREDATOR RESPONSE TO FENCE MODIFICATIONS IN
A GRAZING MODIFIED LANDSCAPE

by

Aaron William O’Harra

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ABSTRACT

Livestock operations are present across much of the greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) current range and the infrastructure associated with this land-use type can have negative effects on sage-grouse populations. Recent work has found that the daily survival rate of nests placed close to fences experience a 4-fold decrease in survival probability. The reduction in survival was theorized to be attributed to higher use of fences by predators due to increased movement efficiency and foraging rates predators experience along linear features. In this study, we experimentally modified fences to reduce perch availability and the barrier effects often associated with fences to improve sage-grouse nest survival. We monitored 177 nests over 8 years to assess the effectiveness of this management technique. We also used camera traps and point count surveys in the last 3 years of the study to assess the occurrence of three common sage-grouse nest predators; badgers (*Taxidea taxus*), coyotes (*Canis latrans*), and avian predators. We modeled daily nest survival against modified and traditional fences and landscape features throughout our study area in a Bayesian framework. Our predator occurrence rates were modeled using a single season occupancy model in relation to similar landscape features used for nest survival modeling. We detected evidence of an increase in nest survival of 11.4% (90% CRI: 3.2%, 20.0%) for sage grouse nests placed closer to modified fences (mean survival = 35.8%) when compared to traditional fence types (mean survival = 24.4%). We also found evidence for a 14% (95% CI: 5%, 23%) decrease in badger occurrence and a 15% (95% CI: 12%, 18%) increase in coyote occurrence along recently modified fences. We found no evidence that avian predators used fences more than areas with no fence present. Our results may be influenced by the distribution of fence types between sagebrush species. Our results indicate that predation risk for sage-grouse nests across a landscape is predator specific. We conclude that modifying fences in this way can improve sage-grouse nest survival, and the effectiveness of these modifications is controlled by a combination of the predators and landscape features associated with a nest site.

CHAPTER ONE

INTRODUCTION TO THE THESIS

Greater sage-grouse (*Centrocercus urophasianus*; hereafter: sage-grouse) are a sagebrush (*Artemisia* spp.) obligate species of the American west. Their range distributions have been declining throughout most of the 20th century (Storch, 2007). Much of this can be ascribed to human caused changes to the landscape. These changes range from habitat loss, to changes in land-use (grazing and agriculture), to the introduction of invasive species (Braun, 1998; Connelly and Braun, 1997; Knick et al., 2015; Storch, 2007). Sage-grouse pre-settlement range used to encompass 1,200,483 km², but is now limited to 668,412 km², 56% of its historical range(See Figure 1-1; Schroeder et al., 2004).

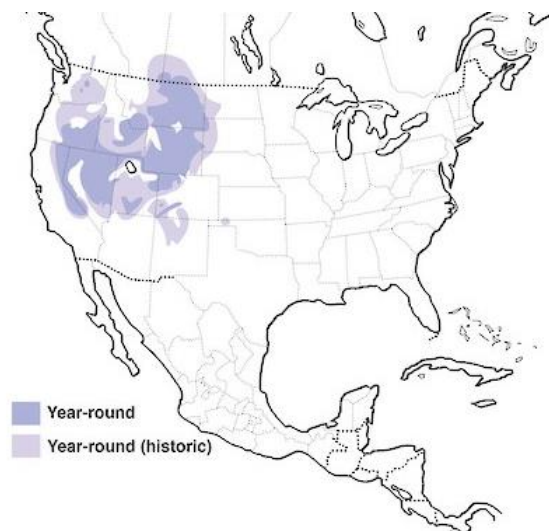


Figure 1-1: Map indicating current and historic range sizes for Greater sage-grouse. Source: Schroeder et al. 2020.

Sage-grouse rely on sagebrush throughout all stages of their life. During the breeding stage, landscapes with a sagebrush mosaic provide ample open sites for lekking along with thick sagebrush dominant vegetation nearby for potential nests and escape cover (Braun et al., 2005; Schroeder et al., 2020). Nest site selection is generally located within 13km of the nearest lek (Hanf et al., 1994). Large tracts of continuous big sagebrush (*Artemisia tridentate* spp.), grass, and herbaceous cover are needed to provide concealment during the nesting stage of a sage-grouse life cycle (Braun, 1998; Cutting et al., 2019; Schroff et al., 2018). Sagebrush with larger canopies and higher grass cover are often selected at the fine scale nesting site (Connelly et al., 2000; Schroff et al., 2018).

A sage-grouse nest consists of a shallow depression dug or scratched into the ground beneath the nest shrub (Schroeder et al., 2020). After breeding, sage-grouse generally lay between 6 to 10 eggs per nesting attempt (Connelly et al., 2000). The average incubation period is 28 days (Cutting et al., 2019; Moynahan et al., 2007; Taylor et al., 2017), with the adult spending around 96% of this time on the nest (Coates and Delehanty, 2008).

Sage-grouse brood rearing relies on sagebrush and the relative abundance of forbs and insects that grow within the sagebrush steppe ecosystems. Sage-grouse chicks depend heavily on forbs and insects for survival at a young age, before sagebrush begins to play the major role in their diet (Klebenow and Gray, 1968). In the winter months, sagebrush is the main food source, making up 99% of a sage-grouse diet (Braun et al., 2005; Wallestad and Eng, 1975). This can be attributed to the accumulation of snow which leaves large species of sagebrush as the only food source available in much of the sage-grouse wintering range. Besides diet, sagebrush creates

structure that is important during brood rearing, providing vertical and horizontal cover from potential predators (Gregg and Crawford, 2009).

Throughout most of the sage-grouse range, livestock grazing is the most common land use practice (Knick et al., 2003). High grazing rates have the potential to alter habitats by removing sage-grouse nesting cover and consequentially increase predation rates on nests and broods (Gregg et al., 1994; Monroe et al., 2017). Livestock have caused abandonment of nests, and this increases with an increase in stocking rates (Coates et al., 2008). Livestock occupy much of the sage-grouse habitat and can have negative effects on sage-grouse populations.

With livestock comes a multitude of grazing infrastructure including roads, water tanks, and fences. Fences are a largely understudied aspect of the grazing infrastructure (Jakes et al., 2018). Fences can create large, irregular networks across the landscape and are often the most prevalent linear feature (others include roadways and powerlines). Fences associated with grazing systems can vary from 1-7 strands with differing wire types (barbed-wire, smooth wire, electric fence, etc.), and are often privately owned and maintained. This creates a wide array of fences that are unequal in terms of their effects on the surrounding wildlife. Fences can segregate habitat through their perceived impassability and alterations to animal behavior (Dinkins et al., 2014).

Studies have examined the effect that fences pose to adult sage-grouse including mortalities and barriers to movement (Braun, 1998; Stevens et al., 2012). Limited work has been done assessing the effect of fences on other stages of the sage-grouse life history (i.e. nest and brood survival). A recent study found that daily nest survival is 4 times greater for nests placed >100m from the nearest fence than nests placed next to these structures (Cutting et al., 2019).

This may be attributed to the disproportional use of edge habitats by predator species, increasing the chance of encounter between predators and prey (Murcia, 1995).

In many studies, nest success is cited as the most significant parameter affecting sage-grouse population demographics (Beck and Braun, 1980; Blake, 1970; Crawford and Lutz, 1985; Schroeder et al., 2020). Predation has been noted as the primary source of nest failure in sage-grouse (Moynahan et al., 2007). Recent studies conducted in Wyoming and Nevada have identified ravens (*Corvus corax*), badgers (*Taxidea taxus*), and coyotes (*Canis latrans*) as the most common sage-grouse nest predators, with predation rates on nests of 35%, 34%, and 19% respectively (Conover and Roberts, 2017). These predators are more often detected in areas with high surface disturbance (Sanders and Chalfoun, 2019) attributed to human modifications.

Avian predation has been subsidized through livestock grazing by providing additional perches throughout a once open landscape and providing anthropogenic food sources from roadkill (Forman and Alexander, 1998; Lambertucci et al., 2009). Common ravens are a generalist predator, meaning they have primary food sources but will also find and utilize opportunistic food sources within their home range. Common ravens rely mainly on visual cues to locate eggs and young of many of their prey species (Coates and Delehanty, 2010). Unlike sage-grouse who have declined with human expansion, raven numbers have increased nearly 300% since the year 1980 (Sauer et al., 2013). Ravens have increased their numbers in the sagebrush steppe ecosystem (Coates et al., 2014) and are taking advantage of the abundant artificial perching structures. These structures include power poles, buildings, fences, and water tanks (Braun, 1998; Coates et al., 2014; Kristan and Boarman, 2007; Manzer and Hannon, 2005).

Anthropogenic perch sites are facilitating the hunting of prey by avian predators by offering a heightened view of the surrounding landscape.

Fences act as travel corridors for many ground predators with the potential to predate sage-grouse nests (Braun, 1998). These fences create added edge effects that would otherwise be limited to roadways and differing/fragmented habitat types. Both badgers and coyotes are generalist predators (Roper, 1994; Sacks and Neale, 2002) and fit into the mesocarnivore guild. Vold and McNew (2018) found a higher use of fences by mesocarnivores based on the improved foraging efforts (lower effort for greater prey capture rates) they experience at these locales. Coyotes specifically have been found to commonly use fences and edge habitats to enhance their foraging efficiency (Atwood et al., 2004). These linear features on the landscape have also been shown to enhance a predator's movement efficiency, allowing them to travel faster and further throughout the landscape (DeMars and Boutin, 2018; Dickie et al., 2020, 2017). This increases their likelihood of encountering prey species, holding high implications for the effect of grazing system infrastructure on sage-grouse populations. Higher predation rates along fences is a likely cause of the lower nest survival rates in these areas (Cutting et al., 2019).

Current modifications for sage-grouse are limited to the placement of fence markers along wires. These markers are intended to increase the visibility of fences and lower the risk of collision (Van Lanen et al., 2017). This management tactic reduces collision caused mortalities but still leaves the increased effect of predation along fences unaltered. The impacts of fences on the survival of sage-grouse have been minimally studied and are currently a research priority (Hovick et al., 2014).

We performed a large-scale experiment that modifies existing fences to reduce the anthropogenic subsidies that fences have been shown to provide for common predators of sage-grouse nests. In Chapter Two, we assess the nest survival rates of sage-grouse in relation to modified and traditional fence types. We then assess how fences and their modifications affect common predators of sage-grouse nests in Chapter Three. In Chapter Four we use the results from the previous two chapters to characterize the differing predation risks across our study site for sage-grouse nests in relation to their common nest predators. Our work promotes the use of simple fence modifications to improve a key vital rate for a sagebrush species of concern.

CHAPTER TWO

LARGE SCALE FENCE MODIFICATIONS INCREASE NEST SURVIVAL IN GREATER
SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*)

Contributions of Authors and Co-Authors

Manuscript in Chapter Two

Author: Aaron W. O’Harra

Contributions: Conceived idea, study design, and performed data collection. Analyzed the data and wrote the paper.

Co-Author: Kyle A. Cutting

Contributions: Conceived idea, study design, and performed data collection. Analyzed the data and wrote the paper.

Co-Author: Jason D. Tack

Contributions: Analyzed the data and wrote the paper.

Co-Author: Michael R. Frisina

Contributions: Outlined and wrote the paper.

Co-Author: Bok F. Sowell

Contributions: Conceived idea and study design. Outlined and wrote the paper.

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Aaron W. O’Harra, Kyle, A. Cutting, Jason D. Tack, Michael R. Frisina, Bok F. Sowell

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Abstract

Livestock grazing is the most common land-use practice in aridland ecosystems of the American West. Widespread and long-term declines of greater sage-grouse (*Centrocercus urophasianus*), an umbrella species for other sagebrush-associated vertebrates, has challenged land managers to find solutions to help bolster populations. Human infrastructure among western rangelands (e.g. fences) are one potential negative factor on sage-grouse populations, as nest survival – a key demographic vital rate for sage-grouse – can be 4x higher when placed >100 m away from the nearest fence. We implemented the first-ever, large-scale (>94 km in length), controlled experiment designed to evaluate changes in nest survival related to fence modification treatments in southwest Montana, USA. Fence modifications included perch deterrents placed atop fence posts, and raised bottom fence wires (> 45 cm from the ground) intended to reduce the search efficiency of avian and ground-dwelling nest predators. We found that 28-day nest survival within 100m of a modified fence may be increased by an average difference of 11.4% (90% CRI: 3.2%, 20.0%) from rates seen along traditional fences using a Bayesian framework. The difference in nest survival between fence types (modified vs. traditional) appeared greater for modified fences in both low elevations and sites closer to mesic meadows or streams. However, the distribution of nests and fence types may have influenced these results. Our findings suggest that modifying fences designed to reduce the search efficiency of avian and ground-dwelling predators will likely benefit nest survival in sage-grouse across the sagebrush biome. This fence modification technique offers practitioners a tool to advance grazing practices, while reducing conflict between human infrastructure and wildlife conservation.

Introduction

Livestock grazing is one of the most widely applied land-uses in the American West, with much of it occurring in sagebrush steppe ecosystems. This creates high potential for overlap between livestock grazing and greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) populations, an important indicator species for sagebrush (*Artemisia spp.*) ecosystem health. One of the most ubiquitous features of grazing is the addition of human infrastructure used to facilitate livestock grazing programs (Briske et al., 2011; Fleming and Bateman, 2018). Permanent linear-and-point infrastructure (hereafter LPI) – including water tanks, roads, and fences – are critical tools used to control the spatio-temporal patterns of livestock grazing. Yet, empirical studies on LPI including fence designs and their effects on wildlife survival and behavior are sparse (Hovick et al., 2014).

Grazing systems are dependent upon human infrastructure (Cutting et al., 2019). There are millions of miles of fence used in grazing systems in the American West, even exceeding total road distance in many areas (Jakes et al., 2018). Fences are linear infrastructure features with vertical posts that hold noncontinuous structures (e.g. wire) that connect the interspace (McInturff et al., 2020). Fence types common to sagebrush ecosystems include smooth, barbed, electric, woven wire, and wooden. Fences can be a valuable tool for controlling the distribution of livestock and for protection of sensitive areas (Bailey, 2004), conversely fences can be harmful as they can negatively influence wildlife populations either directly (e.g. collisions, mortality, hair loss; Harrington and Conover, 2006) or indirectly (e.g. behavioral changes, obstructed movements; Jakes et al., 2018). Fences are spatially distributed, differ in density, condition, and type, and create varying vertical and horizontal obstacles for the many wildlife

species that encounter them (Jakes et al., 2018). Anthropogenically created linear features (i.e. roads and fences) have recently been shown to facilitate movement patterns of predators, as use of these features allows predators to travel faster and farther throughout landscapes (Dickie et al., 2020, 2017; Prugh et al., 2009). Yet, understanding the impacts of predator use of LPI on subsequent prey survival across a range of landscape topographic complexity remains elusive.

Previously, mortality caused via collisions with fences was one of the few identified (and since mitigated; Van Lanen et al., 2017) risks LPI posed to sage-grouse survival. Recent research however, indicates a link between grazing-related LPI, predator movement behavior, and survival of ground dwelling birds (Andersson et al., 2009; Cutting et al., 2019). In human modified landscapes, predators are able to use LPI to increase their foraging efficiency through increased search efficiency and handling time of prey (McCauley et al., 1993). Predation is the leading cause of nest failure in ground nesting birds (Donovan and Thompson, 2001; Martin and Roper, 1988; Moynahan et al., 2007; Okada et al., 2019). Cutting et al. (2019) found that sage-grouse nests placed close (<100m) to fences display a four-fold reduction in survival in comparison to nests located further away (>100m). This finding merits further research as sage-grouse are a primary focal point for conservation and management of sagebrush ecosystems and influence rangeland management policy across western North America (Smith et al., 2020). Understanding changes in predator-prey interactions in response to experimental modification of fences is an important first step in developing conservation plans and adding to the emerging field of '*fence ecology*' (McInturff et al., 2020).

Furthering understanding of impacts of fences on demographic rates of prey can be achieved through experiments that scramble the search efficiency of predators. For example, the

three dominant nest predators of sage-grouse, including coyotes (*Canis latrans*), badgers (*Taxidea taxus*), and ravens (*Corvus corax*) (Conover and Roberts, 2017), use fences to increase movements and foraging efficiency (Coates et al., 2016; Hovick et al., 2014). Coyotes commonly use fences and edge corridors to enhance movements in search of food (Atwood et al., 2004), while ravens use vertical LPI for perches that can improve visibility and allow for less energy expenditure (Andersson et al., 2009). Yet, no studies have experimentally modified fences to reduce predator foraging efficiency with the goal of improving nest survival in ground nesting birds.

In this research, we used long-term data (8-years) on a radio-marked population of sage-grouse to evaluate a large-scale experiment on fence design to assess 1) if the influence of fences on sage-grouse nest survival is altered with experimental fence modifications intended to reduce efficiency of nest predators, and 2) whether experimental fence modifications influence nest survival differently across topographic gradients and other grazing-related LPI. We hypothesized that experimental fence modifications would increase nest survival near fences and this increase would be observed across a range of topographical attributes that characterize the landscape. Our large-scale fence modification experiment aims to provide a novel design that can reduce impacts of fences on nest survival for sage-grouse, a species that drives many land use decisions across the American West.

Methods

Study Area

This study was conducted across a high-elevation sagebrush landscape site (1,560 km²) located in southwestern Montana, USA (Figure 2-1). The site is located within the Centennial Valley, MT, USA sitting with a base elevation of 2,000m. The average annual precipitation and temperature is 50cm and 1.6°C, respectively. Many land ownerships exist throughout the area, including private and public entities such as the Red Rock Lakes National Wildlife Refuge. There are three dominant sagebrush species present throughout the study site consisting of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*), and three-tip sagebrush (*Artemisia tripartita*). The predominant land-use practice of the area is livestock grazing, with most of the landscape receiving grazing activity. Most of the study site is on a rest-rotation grazing system, with pastures being grazed for 2-3 years followed by a year of rest. Average stocking rate varied from 1.2-2.0 ha per adult cow with an average weight of 454 kg (Cutting et al., 2019).

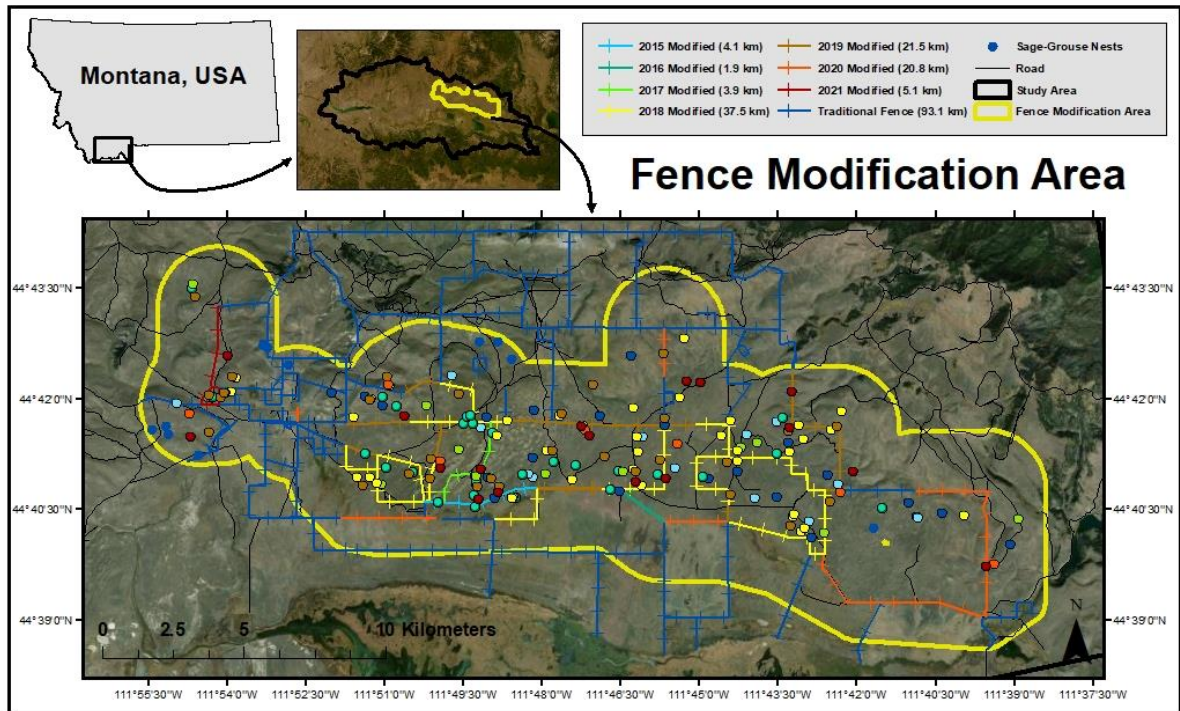


Figure 2-1: Experimental fence modification area (FMA) and nest site locations of female sage-grouse. The FMA is located in southwest Montana, USA. Inset shows years when fence modification occurred, along with proximity to traditional fences. Nests are color coded the same as fences by year. Nests shown in blue are from the year 2014. This treatment was performed as a management action, resulting in many fences being modified centrally where previous studies had found lower survival of sage-grouse nests.

Fence Modifications

Approximately 95km of fence were modified in the project area between the years 2015-2021. The fence modification area (FMA) is located in the northeastern portion of the study site and encompasses roughly 125km² (Figure 2-1). We defined the FMA to be within 1.5km of a modified fence, creating an area where both fence types are represented at roughly equal lengths (95km of modified fence and 93km of traditional fence). Modifications were implemented as a management action, and were initially focused in the lower elevation BBSA dominated sites before adding the treatment in other sagebrush types. Modifications to fences include bundles of

sharp metal spikes placed atop fence posts to preclude landing by aerial predators (perch deterrent; Nixalite®) and raising the bottom wire to 45cm above ground level to reduce edge effects used by ground nest predators to hunt more effectively (Figure 2-2). We considered traditional fences to comprise of all fences not modified with perch deterrents that consist of multi-strand barbed or smooth wire, woven wire, or wooden fences.

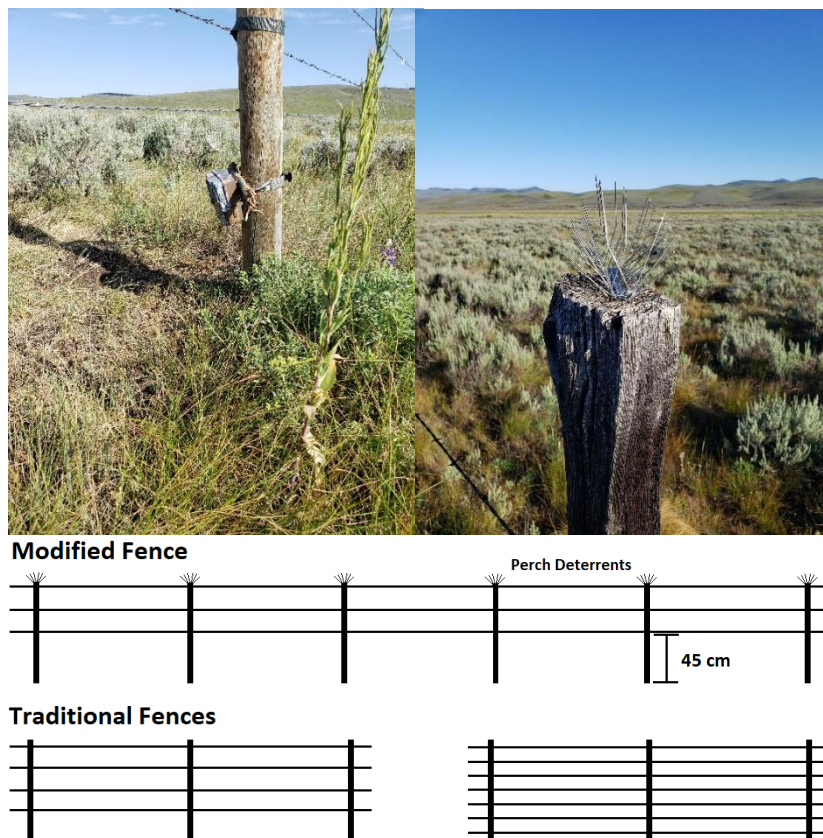


Figure 2-2: An example of the raised lower wire is shown in the top left image. The camera in the image is ~11cm for reference. In the top right image is an example of Nixalite® fixed to the top of a wooden post using fence staples. The diagram at the bottom indicates the two modifications needed to consider a fence modified in comparison to two examples of traditional fences that could be encountered. Photograph credits: A. O’Harra.

Female Sage-grouse Capture and Monitoring

Adult female sage-grouse were captured across 10 breeding leks located throughout the study area between 2014-2021. Spotlighting and net techniques were used to capture female sage-grouse near their leks. Once captured, each bird was fitted with a VHF necklace style radio transmitter ranging in weight from 22 g (Advanced Telemetry System, Isanti, MN), 15 g (Holohil Systems Ltd., Carp, Ontario, Canada), and 12 g (American Wildlife Enterprises, Monticello, FL). All transmitter models weighed less than weight thresholds known to affect flying animals (<5% total body weight; Cochran, 1980). Females were tracked 2-3 times per week from mid-April through mid-July using intensive ground surveys and aerial surveys as needed to locate missing birds. A nest was confirmed when a female was located in the same location for 2 consecutive occasions. Once a nest was located, we monitored it 2 times per week until the fate was determined as either successful (≥ 1 egg hatched) or unsuccessful. To reduce human disturbance at the nest site we established listening points placed between 50-100 m away to monitor the nest until the fate was determined. Six nests were abandoned due to investigator disturbance and were censored from analyses. Research was conducted in compliance with state (2014-050, 2015- 23, 2016-049, 2017-043, 2018-003, 2019-078, 2020-010-W, 2021-026-W) and animal care and use (2012-40, 2015-30, 2019-88) permits.

Statistical Analyses

Within the FMA, we selected nests from all years located within 1 km of either fence type for analyses. This focuses our analyses to those nests that are close enough for potential influences of fence type allowing us to address the following two objectives: 1) evaluate fence

modifications on nest survival, and 2) whether fence modifications influence nest survival similarly across space and time.

Model Covariates: Predictor variables used to evaluate variation in nest survival included fence type (i.e. modified or traditional) and distance, distance from other LPI (i.e. water tanks, roads), topographic variables (elevation, heatload, and compound topographic index), and nest incubation initiation date (*hereafter* initiation date) (Table 2-1). We used elevation in place of sagebrush type as the latter are found across a predictable elevation gradient (Figure 2-3). Information on the locations of fences, roads, and water tanks throughout the FMA were compiled using existing data. Locations and structure types were verified to be accurate through field surveys. We used ArcGIS10.6.1 (ESRI, Redlands, California, USA) to measure linear distances from nests to LPIs.

Table 2-1: Covariates used in daily survival analysis of sage-grouse nests.

| Variable | Category | Description | Type |
|-----------------|-----------------|---|-------------|
| Fence Type | LPI | Modified or traditional | Binary |
| Fence | LPI | Distance to fence | Continuous |
| Road | LPI | Distance to road | Continuous |
| Water Tank | LPI | Distance to water tank | Continuous |
| Initiation Date | Temporal | Ordinal date when nest incubation was initiated | Continuous |
| Elevation | Topographic | Proxy for sagebrush type | Continuous |
| Heatload | Topographic | Combination of slope and aspect | Continuous |
| CTI | Topographic | Index for moisture content | Continuous |

*LPI: Linear Point Infrastructure

*CTI: Compound Topographic Index

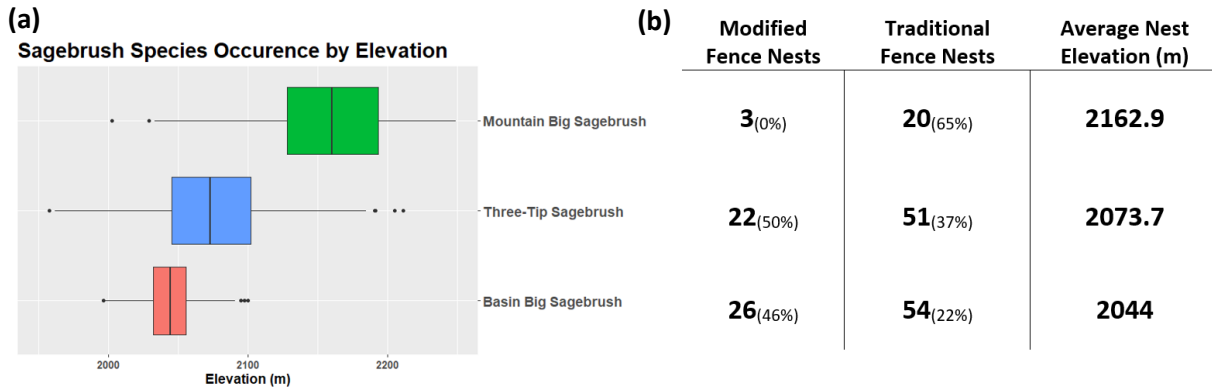


Figure 2-3: Sagebrush types occur across a predictable elevational gradient (a). Number of nests per sagebrush type that were nearest to a modified or traditional fence, and the average elevation of the nests that occurred in each sagebrush type (b). Successful nests (%) associated with each fence and sagebrush type is shown in parenthesis (b). One nest was found in low sagebrush (*Artemisia arbuscula*) and is not represented here.

We evaluated whether topographic variables including elevation, heat load index, and compound topographic index (calculated from slope and upstream contributing area; *hereafter* CTI) mediated the effect of fence modifications on nest survival. We calculated elevation using a 30-m² digital elevation model (EROS [USGS Earth Resources Observation and Science Center]. 2016). We calculated CTI and heat load using the geomorphology and gradient metrics toolbox (Evans et al., 2014) in ArcGIS10.6.1. Higher CTI values indicate sites with higher moisture content that can produce greater vegetation growth and create more hiding cover for prey species. Higher heat load values are found on steep, southwest facing aspects that can increase incubation constancy through reduced energy expenditure of incubating females.

We considered date of incubation initiation (date the last egg was laid and incubation started) as a potential predictor to account for temporal variation in nest survival across the nesting season, as nests initiated early in the season experience colder temperatures and earlier stages of vegetation growth than nests initiated later (Klett and Johnson, 1982; Smith et al.,

2018a). The date at which incubation started was calculated by subtracting the average incubation period (28-days; Moynahan et al., 2007) for successful nesting sage-grouse from the hatch date. Since we could not determine the exact initiation date for unsuccessful nests, we subtracted 2.5 days from the date when we first discovered a nest, which was the average days from initiation to discovery in our sample of successful nests.

We predicted that nest survival would be lower for nests placed closer to LPI than those placed further away. We also predicted that nest survival would increase with elevation. Finally, we predicted that nest survival would be higher for nests with incubation initiated in the mid to late season. We tested these predictions by evaluating threshold effects by log transforming LPI variables, elevation, and initiation date. We evaluated support for certain functional forms using the probability of direction (*hereafter* PD) score using the ‘bayestestR’ package (Makowski et al., 2019). PD scores range from 0.5 to 1 and indicate the certainty of an effect for a given covariate on nest survival (Colquhoun, 2014). To estimate the PD on different functional forms for a given covariate on nest survival, we ran models with an intercept and either an original or log-transformed predictor using 3 Monte Carlo Markov chains (MCMC) with 10,000 iterations, discarding the initial 2,000 as burn-in. We selected the functional form for a given covariate that contained the highest PD score (Table 2-2). Prior to running models, we evaluated pairwise correlations among covariates and did not find evidence for high collinearity (Pearson’s $r < 0.70$).

Table 2-2: Probability of Direction (PD) for different functional forms of continuous covariates.

| Covariate | Original | Log |
|-----------------|-------------|-------------|
| Fence | 0.83 | 0.99 |
| Road | 0.68 | 0.79 |
| Water Tank | 0.70 | 0.62 |
| Initiation Date | 0.99 | 0.98 |
| Elevation | 1.00 | 0.99 |

Note: The functional form for a given covariate with the highest PD score is shown in bold.

Nest Survival Model: We used a Bayesian statistical model similar to Schmidt et al., (2010), with binomially distributed errors and an inverse logit link function to model daily survival rate (*hereafter* DSR) of nests among categories of variables related to LPI, topographic variables that describe the biotic sagebrush community, and initiation date. To evaluate the outcome of experimental fence modification on survival, we modeled DSR ($\phi_{i,t}$) as a function of fence type, fence distance, and their interaction for Objective 1 (equation (1)). To evaluate whether topographic complexity found in sagebrush communities influenced the effect of fence modification on DSR, we assessed whether effects of fence type varied spatially or temporally for Objective 2 (equation (2)). We used a Bayesian variable selection technique that uses an indicator variable to quantify the support for effects of each covariate on DSR (Converse et al., 2013). We derived effect sizes of regression coefficients (β) by multiplying each with a binary indicator variable (w) such that:

(1)

Objective 1:

$$\phi_{i,t} = \beta_0 + w_1\beta_1 \times fence.type_i + w_2\beta_2 \times fence_i + w_3\beta_3 \times (fence.type_i \times fence.distance_i)$$

(2)

Objective 2:

$$\phi_{i,t} = \beta_0 + w_1\beta_1 \times fence.type_i + w_2\beta_2 \times fence_i + w_3\beta_3 \times road_i + w_4\beta_4 \times water.tank_i + w_5\beta_5 \times initiation.date_i + w_6\beta_6 \times elevation_i + w_7\beta_7 \times CTI_i + w_8\beta_8 \times heat.load_i + \alpha_j$$

$$\alpha_j \sim N(0, \tau)$$

We scaled the variance of parameter prior distributions to create uninformative priors by creating a mean zero normal prior with variance V/K , where K represents the number of effects present in a model at a particular sample (from 0 to 3 for Objective 1 and 0 to 8 for Objective 2). We placed a Gamma distributed prior on the total variance of the linear predictor, V , with parameters 3.29 and 7.8 as this prior results in a marginal distribution that approximates nest fate outcomes (0,1; Link and Barker, 2006). A Bernoulli (0.5) prior inclusion probability was placed on the indicator variables, which represents no prior knowledge on individual variable importance. This method allows for equal prior probability of the 8 possible model combinations for Objective 1, and all 256 possible model combinations for Objective 2 (Converse et al., 2013). The posterior inclusion probability (w_p ; hereafter PIP) score represents the frequency a given variable was included across all the MCMC simulations. To account for annual effects, we included the covariate *Year* (j) as a random effect (α) from a Normal(0, τ) prior, where τ is a precision parameter from the scaled Gamma(1,2)² distribution. We made inferences based on the top model that included variables with a PIP score > 0.5 , and evaluated parameter estimates and

the extent to which each coefficient in the model overlapped zero. We used model weights to evaluate support for competing models, which are derived from the proportion of MCMC samples for which a particular vector of indicator variables for a given model appeared across all simulations. We selected the top model based on which model had the highest model weight.

For objective 1, we simulated the model using 3 independent Markov chains each with 20,000 samples discarding the initial 2,000 as burn-in. For Objective 2, we simulated the model using 3 independent Markov chains each with 180,000 samples discarding the initial 20,000 as burn-in, using the larger sample size to account for the more complex model. We assessed model convergence by visual inspection and the Gelman-Rubin statistic ensuring \hat{R} was < 1.1 . The models were fit using JAGS (version 4.3.0, mcmc-jags.sourceforge.net, accessed 31 October 2019) via the R2jags package (Su and Yajima, 2015) in program R (version 3.6.1, www.r-project.org, accessed 5 July 2019). Predictions of survival are made across covariates found in the top model by holding other variables constant at their median value, except for distance to fence as we held this covariate at its 1% quantile, as the negative effect of fences on nest survival have been shown to be in the immediate vicinity of a fence (Cutting et al., 2019). Lastly, to assess whether the effect of fence type differed across the range of topographic variables, we tested for interactions between fence type and each topographic variable that was found in the top model.

Results

We discovered 177 nests located within 1 km of a fence located in the FMA from 2014-2021. Fifty-two nests were located nearest a modified fence while 125 were located nearest a traditional fence.

Survival of Nests Across Fence Type and Fence Distance

Our model results indicated that the experimental fence modifications may increase the median overall 28-day nest survival at 100m from a fence by an average of 47% (traditional fence nest survival = 7.9%, 90% CRI: 3.9% – 9.0%; modified fence nest survival = 19.3%, 90% CRI: 7.1% – 29.0%). The top model containing the highest model weight included additive effects of fence type and fence distance (Table 2-3). Both fence type and fence distance appeared to have strong positive effects on DSR (Table 2-4). For example, along modified fences DSR changed from 92.0% to 98.3% (90% CRIs: 89.3% to 94.1% and 96.4% to 99.2% respectively) as the distance between the nest and a fence increased from the 1% quantile (10m) to 99% quantile (990m) in the observed dataset. This equates to nest survival changing from 9.6% to 61.5% (90% CRIs: 4.2% to 18.0% and 35.5% to 79.8% respectively) as distance from a modified fence increases from 10m-990m. In contrast, for traditional fences, DSR changed from 87.9% to 97.3% (90% CRIs: 87.1% to 88.9% and 95.5% to 98.4%) across the same quantiles in the observed dataset (Figure 2-4a). These DSR rates equate to nest survival changing from 2.7% to 46.7% (90% CRIs: 2.1% to 3.7% and 28.0% to 63.9% respectively) with increasing distance from a traditional fence. MCMC chains for all estimated parameters in the models converged ($\hat{R} < 1.1$).

Table 2-3: Candidate models and model weights for daily nest survival (DSR) across fence type and fence distance (a) and space and time (b) of female sage-grouse in southwest Montana, USA.

(a) Model set describing DSR of nests across fence type and fence distance.

| Model | Fence Type | Fence | Fence x Fence Type | Model Weight |
|-------|------------|-------|--------------------|--------------|
| 1 | 1 | 1 | 0 | 0.54 |
| 2 | 0 | 1 | 0 | 0.28 |
| 3 | 0 | 1 | 1 | 0.12 |
| 4 | 1 | 1 | 1 | 0.06 |

(b) Model set describing DSR of nests across space and time.

| Model | Fence Type | Fence | Road | Water Tank | Initiation Date | Elevation | Heat load | CTI | Model Weight |
|-------|------------|-------|------|------------|-----------------|-----------|-----------|-----|--------------|
| 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0.06 |
| 2 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0.06 |
| 3 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0.04 |
| 4 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0.04 |
| 5 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0.03 |
| 6 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0.03 |
| 7 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0.03 |
| 8 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0.03 |
| 9 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0.03 |
| 10 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0.02 |

*CTI: Compound Topographic Index

Notes: Showing model weights for top 4 of 8 possible models in (a), and top 10 of 256 possible models in (b). A “1” and “0” indicates the inclusion and exclusion, respectively, of a given covariate within a given model.

Daily Nest Survival Across Fence Type and Landscape Topographic Variables

The top DSR model containing the highest model weight included the covariates fence type, fence distance, initiation date, elevation, and CTI (Table 2-3). An additional competitive model nearly identical to the top model included the covariate heat load. Heat load had a PIP

score of 0.51, but the estimated effect strongly overlapped zero ($\beta = -0.01$, 90% CRI: -0.38 to 0.40). We therefore made predictions on the top model that did not include the covariate heat load. Nest survival along modified fences appeared greater with increasing initiation date, elevation, and CTI values. For initiation date, DSR was higher along modified fences (median = 94.4%; 90% CRI: 88.9% to 97.6%) than traditional (median = 92.9%; 90% CRI: 86.0% to 96.8%; Figure 2-4b), however the CRIs overlap significantly, indicating the effect of modified fences doesn't outweigh changes in DSR related to initiation date. For elevation and CTI, we found support for the interaction of both covariates with fence type (PIP scores of 0.59 and 0.57, respectively). DSR for nests in lower elevations (1% quantile in observed dataset = 2,028m) was higher for nests along modified (95.3%; 90% CRI: 95.3% to 95.3%) than traditional fences (93.4%; 90% CRI: 93.3% to 93.4%), but the difference in DSR became more similar between fence types in higher elevations (99% quantile = 2260m; DSR: modified = 98.0%; 90% CRI: 96.9% to 98.9% vs. traditional = 97.1%; 90% CRI: 95.5% to 98.4%; Figure 2-4c). The difference in DSR of nests along modified vs. traditional fences was greater as the value of CTI increased (Figure 2-4d). For example, the difference in DSR between fence types for nests in areas with lower CTI values (1% quantile) was roughly 1.9% (modified = 91.2%; 90% CRI: 89.5% to 92.6% vs traditional = 89.3%; 90% CRI: 87.3% to 90.9%). The difference became more pronounced at 4.2% in areas with higher CTI values (99% quantile; DSR: modified = 97.3%; 90% CRI: 94.3% to 99.1% vs. traditional = 93.1%; 90% CRI: 86.1% to 97.7%). MCMC chains for all estimated parameters in the models converged ($\hat{R} < 1.1$).

Table 2-4: Parameter estimates and credible intervals (CRI) from the top models, (a) and (b), describing daily nest survival (DSR) of sage-grouse.

(a) DSR across fence type and fence distance.

| Parameter | PIP Score | Estimate | Lower 90% CRI | Upper 90% CRI |
|------------------------|-----------|----------|---------------|---------------|
| β_0 (intercept) | – | 1.72 | 1.18 | 2.30 |
| β_1 (fence type) | 0.57 | 0.45 | 0.11 | 0.79 |
| β_2 (fence) | 0.98 | 0.28 | 0.16 | 0.39 |

(b) DSR across space and time.

| | | | | |
|-----------------------------|------|------|-------|------|
| β_0 (intercept) | – | 0.06 | -0.35 | 0.50 |
| β_1 (fence type) | 0.64 | 0.28 | -0.04 | 0.62 |
| β_2 (fence) | 0.74 | 0.14 | 0.02 | 0.25 |
| β_5 (initiation date) | 0.99 | 0.02 | 0.01 | 0.02 |
| β_6 (elevation) | 0.90 | 0.27 | 0.10 | 0.46 |
| β_7 (CTI) | 0.64 | 0.09 | 0.01 | 0.18 |

*PIP: Posterior Inclusion Probability

*CTI: Compound Topographic Index

Discussion

Previously, fences have been shown to influence sage-grouse population dynamics through collision caused mortalities (Harrington and Conover, 2006), yet fences can also indirectly reduce nest survival. Nest survival is one of the most influential vital rates for sage-grouse population growth (Taylor et al., 2012). Our modeling approach highlights the importance of landscape variables on the effectiveness of fence modifications at increasing DSR along a gradient of elevation and CTI values. At low elevations, fence modifications had strong effects on increasing DSR, but this effect appears to lessen with increasing elevation. We

observed a similar result with CTI values indicating a positive effect of fence modification on DSR in areas with more potential wetness. Timing of nest initiation also appeared to affect DSR as nests initiated late in the season experienced higher survival rates than those initiated early, this result however is not strongly supported given the overlap seen in the 90% CRIs. The effect of initiation date on DSR did not appear to be influenced by the fence type a nest is closer to (Figure 2-4b).

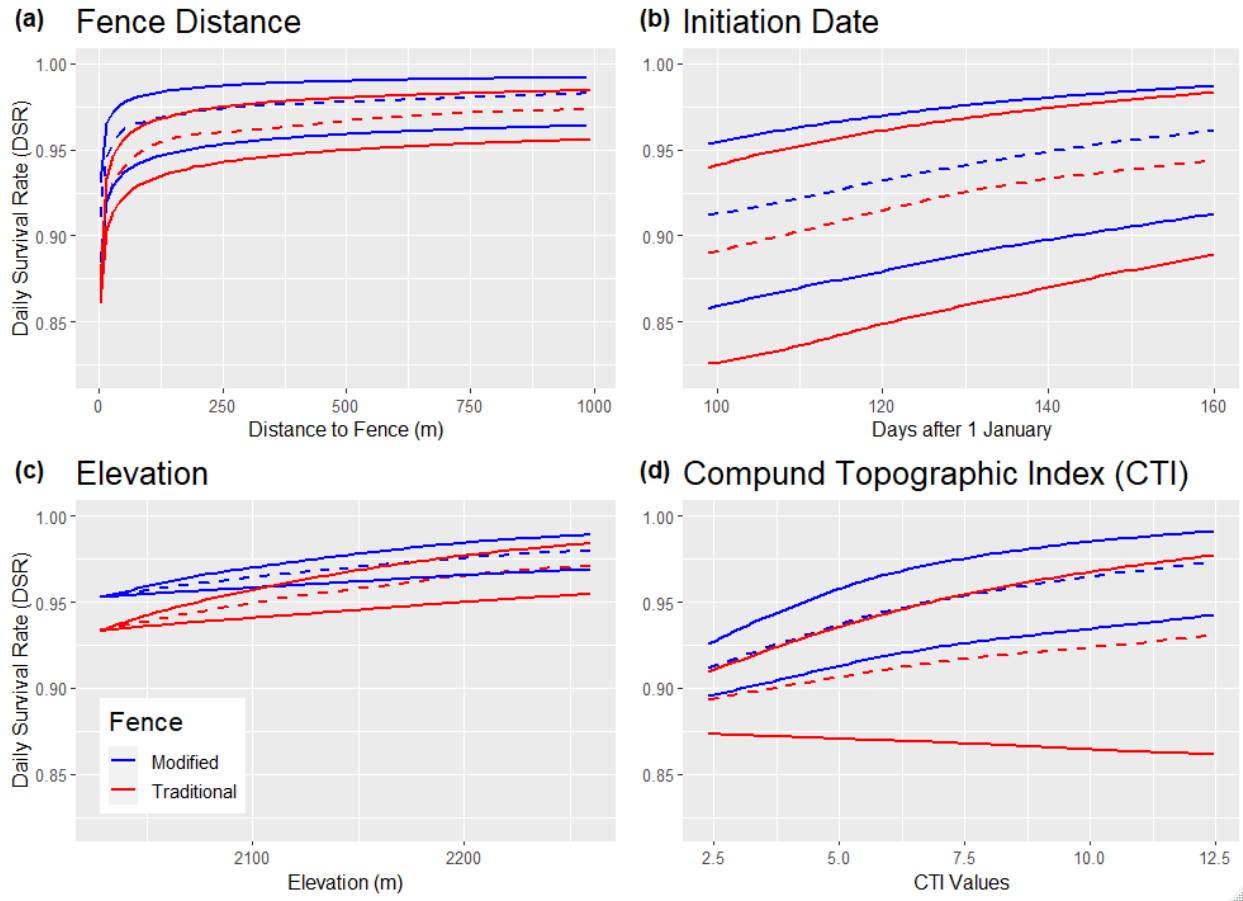


Figure 2-4: Predicted daily survival rates (DSR) for sage-grouse nests across different fence types including modified (blue) and traditional (red) in relation to distance to fence as modeled in objective 1 (a), initiation date (b), elevation (c), and compound topographic index (CTI) (d). Each covariate was plotted over the range of values in our dataset with other covariates held at their mean value, while distance to fence was held at the 1% quantile in the observed dataset for plots b-d. The dashed lines represent the median effect of each fence type and the solid lines represent the 90% CRIs. Plots c and d represent the interaction between fence type and their respective covariate.

Our data leave open the possibility that the change in DSR seen across the landscape could be due to different assemblages of aerial and ground nest predator communities. With unknown abundances of predators in our study system, it is likely that predation pressure on nests is heterogeneous. Higher elevation areas oftentimes have more trees at this study site, increasing perch numbers and perch heights for aerial nest predators. Prey detectability for aerial

predators is improved with increases in viewing height (Andersson et al., 2009). Coyotes on the other hand have lower successful prey capture attempts in more forested areas (Gese et al., 1996). With higher DSR of nests that we observed with increasing elevations, ground predators may be the dominant contributors to nest predation in this study system, and the predation risk they pose is greater in lower elevations (Cutting et al., 2019). The increase in DSR of nests observed with increasing elevations is also tied to the dominant sagebrush species. Mountain big sagebrush becomes dominant at higher elevations in our study system (Figure 2-2), which has the greatest amount of herbaceous cover among all sagebrush species at our study site (Schroff et al., 2018). Cutting et al. (2019) found that areas dominated with mountain big sagebrush have significantly higher nest survival than sites dominated by basin big sagebrush, which occurs at lower elevation valley bottoms. Different sagebrush types or nest predator assemblages across elevations or both are plausible explanations to the response observed in DSR of nests.

In wetter sites (e.g. mesic meadows), represented here as areas with higher CTI values, coyotes have been found to have higher predation rates, presumably because prey populations congregate in these wetter sites (Gese et al., 1996). We found that modified fences appear to increase DSR of nests more effectively in areas that have higher moisture potential than nests found in arid sites (Figure 2-4d). This may indicate that in our study system predators utilize wetter (mesic) sites more frequently than their drier counterpart in the adjacent uplands. In high elevation sagebrush steppe, mesic meadows can be important refugia for many species that rely on a high diversity of forbs and insects for food resources that persist later into the growing season. Overall, these results indicate that modifying fences in wetter, more mesic areas containing higher CTI values may be an important management tactic to consider for managing

continuous sage-grouse habitats including lekking and nesting areas (Holloran and Anderson, 2005).

Predator-prey dynamics are also likely to shift as the sage-grouse nesting season progresses. Later in the nesting season there is generally more abundant alternative prey sources, such as rodents and other avian species that initiate nesting later than sage-grouse. This likely influences the increase in DSR seen with nests initiated later in the season via the alternative prey hypothesis (Wegge and Storaas, 1990). Vegetative phenology also progresses with the nesting season and provides greater concealment of nests initiated later (Smith et al., 2018b). Alternative prey and greater amounts of hiding cover are both possible explanations as to why DSR appears to increase with later initiation dates.

Advancing Grazing Practices for Sage-Grouse Conservation

The positive effect of these novel fence modifications on nest survival found herein advances sustainable grazing systems. Cutting et al. (2019) originally showed a positive effect of distance to fence on nest survival. Our study differed however by implementing a large-scale experiment, and by adding 5 additional years of data. Regardless, these differences still resulted in the same finding showing fences reduce nest survival in sage-grouse across long periods (8 years). The most prominent effect of modified fences was seen in areas where DSR was relatively low (i.e. <100m from a fence; Figure 2-4a). The lines of evidence here favor the idea that the improved foraging efficiency of both aerial and ground predators along fences is a driving factor in reducing nest survival near these structures. This learned predator behavior appears altered through modifying fences like those carried out in this study, resulting in the increase in nest survival. Understanding the relationship between predators and fence

modifications across a topographically diverse landscape could be key to improving our understanding of prey species survival. In a tandem study, we were assessing this idea by evaluating predator assemblages along modified and traditional fences (Chapter 3). Indirect effects are generally more difficult to conceptualize and measure but doing so is critical as they can be just as substantial as the direct effects of fences on wildlife (Kristov, 2008).

The current predator assemblage seen today has evolved with the presence of fences, and their utilization of this infrastructure type has likely increased from the anthropogenic subsidies fences can provide. While fences appear to facilitate predation of sage-grouse nests, future work should consider whether this conclusion can be generalized to other ground nesting species and geographic sites with varying levels of topographically diverse features used by nesting grouse. A simplification to the experimental design where only one modification is utilized may also prove adequate, however knowledge of the suite of predators and unique landscape factors in an area would be required to guide that decision. We managed to achieve similar structure for modified fences, but traditional fence structures were dependent on who built the fence, its intended purpose, and the materials used in construction. The higher degree of variation in traditional fence structures likely holds influence over predator behavior and subsequent nest survival. Variation in fence structure was not able to be assessed in our modeling efforts, but future studies should take different fence structure types into consideration. An in depth understanding of the relationship between predators, their prey, and fences is needed to progress the field of fence ecology.

Fencing for livestock is one of the most ubiquitous fence uses throughout the world, yet proportionately understudied (McInturff et al., 2020). With most fence construction being

unregulated, owned, and maintained mostly by private landowners (Jakes et al., 2018), it is no wonder that new fences are often constructed with minimal specificity in terms of their role to conservation, and the short-term functions are prioritized over the long-term outcomes (Sun et al., 2020). With roughly one third of our nests having occurred on private lands, public and private collaborations centered on fence design and construction are necessary to mitigate the negative effects already documented of fences on wildlife. We strongly encourage collaborations of this type that could expand this management tactic across large landscapes, thereby improving a key vital rate for sage-grouse, and perhaps other ground dwelling birds, while maintaining profitability for the livestock community. Fences are continuing to proliferate with greater than an estimated 1 million kilometers of fence already present across the American West (McInturff et al., 2020). This highlights the potential for population level impacts from both the direct and indirect effects of fences and this should be a current research priority of utmost urgency, especially in working landscapes. Novel yet simple fence modifications like those described herein should make this technique achievable across various stakeholders including conservation programs, livestock producers, and land practitioners, given fences are the primary technique for managing the spatio-temporal patterns of livestock.

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CHAPTER THREE

GREATER SAGE-GROUSE PREDATOR RESPONSE TO FENCE MODIFICATIONS IN A
GRAZING MODIFIED LANDSCAPEAbstract

Linear features on the landscape (i.e. roads and fences) have been shown to facilitate increased travel rates and foraging efficiencies for predators. This increased use of linear features poses threats to the prey species these predators may encounter. Greater sage-grouse (*Centrocercus urophasianus*), an important indicator species for sagebrush ecosystems, may be negatively affected by this increase in predator use of fences. Recent work has found that nest survival is significantly reduced within 100m of a fence and expected that decrease in survival to come from the increased predator usage. We experimentally modified 95km of fence in the Centennial Valley of southwest Montana. Modifications included a perch deterrent placed atop fence posts and the lowest wire raised to a height of 45cm above the ground. We monitored three different common sage-grouse nest predators (coyotes - *Canis latrans*, badgers – *Taxidea taxus*, and avian species) to assess how they respond to this modification (n = 147) compared to traditional fences (n=153). We accounted for other grazing and topographic related features of the landscape using a single-season single-species occupancy model. We found that coyote occurrence increased along modified fences whereas badger occurrence decreased. We found no evidence that avian predators used fences more than the surrounding landscape, but due to low sample sizes we could not compare occurrence between fence types. We found that the dominant sagebrush type influenced the occurrence probabilities of our three predators. Coyotes were the only predator where occurrence was greatest in the sagebrush types where nest survival of sage-

grouse was lowest. We speculate that coyotes may be the most likely nest predator of sage-grouse nests within this study area.

Introduction

Predator communities have been altered dramatically in the last century due to human expansion into natural systems (Jachowski et al., 2020). One of the most significant changes is the expanding distribution and abundance of many generalist predator species (Newsome et al., 2015). Mesopredators and many avian predator species are considered generalists, which have been shown to experienced benefits from anthropogenic food sources or habitat that would otherwise not exist in an unaltered landscape (Sovada et al., 2001). The expansion of generalist predators poses threats to the prey species they encounter, especially those species not well-adapted to environmental change (Kristan and Boarman, 2007).

In sagebrush-steppe ecosystems of the American West virtually all sagebrush lands are managed for the principle use of livestock grazing (Fleischner, 1994; Knick et al., 2003). Livestock can reduce vegetative cover, reducing cover for predators stalking prey, and change the plant communities, altering prey availabilities across the landscape (Fleischner, 1994; Vavra, 2005). Beyond the ability of livestock to alter vegetation communities and composition, livestock operations require a multitude of grazing infrastructure, seen with the addition of roads, water tanks, and fences to the landscape. Grazing infrastructure can reduce habitat quality through fragmentation, barrier effects, and the intrusion of edge effects in natural systems (Benítez-López et al., 2010; Forman and Alexander, 1998; Jakes et al., 2018). Grazing systems have been found to increase use by mesopredators, with these predators more frequently found

occupying areas near human added linear features (Gese and Thompson, 2014; Vold et al., 2019). The magnitude and direction of these effects can vary, dependent on the predator-prey interactions at play in an ecosystem.

Linear features, such as fences and roads, have recently been shown to facilitate movement patterns of predators, as use of these features allows for faster and further travel throughout the landscape (Dickie et al., 2020, 2017; Prugh et al., 2009). For example, wolf travel rates were over 100m/15min faster along linear features compared to undisturbed habitats (Dickie et al., 2020). Facilitated movement in grazing landscapes can induce higher predation risk for a multitude of prey species across large areas. Understanding selection preferences of predators in regards to these features can be critical to prey species management.

Fences are an understudied aspect of grazing infrastructure (Jakes et al., 2018). Fences can create large, irregular networks across the landscape and are often the most prevalent linear feature. Fences have the potential to segregate habitats through their perceived impassability and alterations to animal behavior (Dinkins et al. 2014). Fences associated with grazing systems can vary from 1-7 strands with differing wire types (barbed-wire, smooth wire, electric fence, etc.), and are often privately owned and maintained. This creates a wide array of fences that differ in terms of their effects on the surrounding wildlife.

Recently, Cutting et al. (2019) found fences had a negative effect on nest survival of greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse'). Sage-grouse are a sagebrush indicator species of high conservation concern (Conover and Roberts, 2017) and nest success has been cited as one of the most significant parameters affecting their population dynamics (Beck and Braun, 1980; Blake, 1970; Crawford and Lutz, 1985). The leading cause of

sage-grouse reproductive failure is the predation of nests (Moynahan et al., 2007). Cutting et al. (2019) suggested that increased predation along fence corridors is a likely cause of the lower nest success in these locales. Three species of generalist predators, common ravens (*Corvus corax*), badgers (*Taxidea taxus*), and coyotes (*Canis latrans*), have been documented as the most common nest predators of sage-grouse throughout their range (Conover and Roberts, 2017). The dominant nest predator was variable throughout the sage-grouse range, with areas of Nevada finding ravens were the most common nest predator (Coates et al., 2008), whereas a study in the Bighorn Basin of Wyoming found coyotes to be the most common nest predator (Taylor et al., 2017). Mesopredators, i.e. badgers and coyotes, have been found to utilize fences more frequently than surrounding landscapes due to the improved foraging rates they experience along these structures (Vold and McNew, 2018). Little is known about how avian predators respond to fences, but we theorize they may benefit from the large addition of perches throughout what were once relatively open landscapes.

With fences providing subsidies for predators, what then will be made of the prey species that utilize areas near fences? In this study, we have modified existing fences on the landscape with the goal of reducing the subsidies that fences provide for common predators of sage-grouse nests. We completed a large-scale management action that reduced both the availability of perches and the barrier effects often associated with fences. Our objectives were to assess 1) how occurrence rates of both ground and avian predator change in relation to grazing infrastructure and natural features at our study site, and 2) compare the relative occurrence of ground predators on modified fences to those with no modifications completed. The inclusion of fences in studies of wildlife populations is a relatively new concept, with little research having been done in the

field of fence ecology (Jakes et al., 2018). Using sage-grouse as an example, we will discuss how our results may impact prey populations.

Methods

Study Area

Our study was conducted at a 125 km² site located in southwestern Montana, USA (Figure 3-1). This site encompasses the sandhills region of the Centennial Valley which has a base elevation of 2000m increasing to 2500m at its highest. The average annual precipitation and temperature is 50cm and 1.6°C, respectively. Many different land ownerships exist throughout the area, including private landowners and public lands such as the Red Rock Lakes National Wildlife Refuge. The site is characterized by three main sagebrush types; mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*; here-after ‘MTSA’), basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*; here-after ‘BBSA’), and three-tip sagebrush (*Artemisia tripartite*; here-after ‘TTSA’). The predominant land-use practice of the area is livestock grazing, with most of the landscape receiving annual grazing activity. Some of the study site is on a rest-rotation grazing system, with pastures being grazed for 2-3 years followed by a year of rest. Average stocking rate varied from 1.2-2.0 ha per adult cow with an average weight of 454 kg (Cutting et al., 2019).

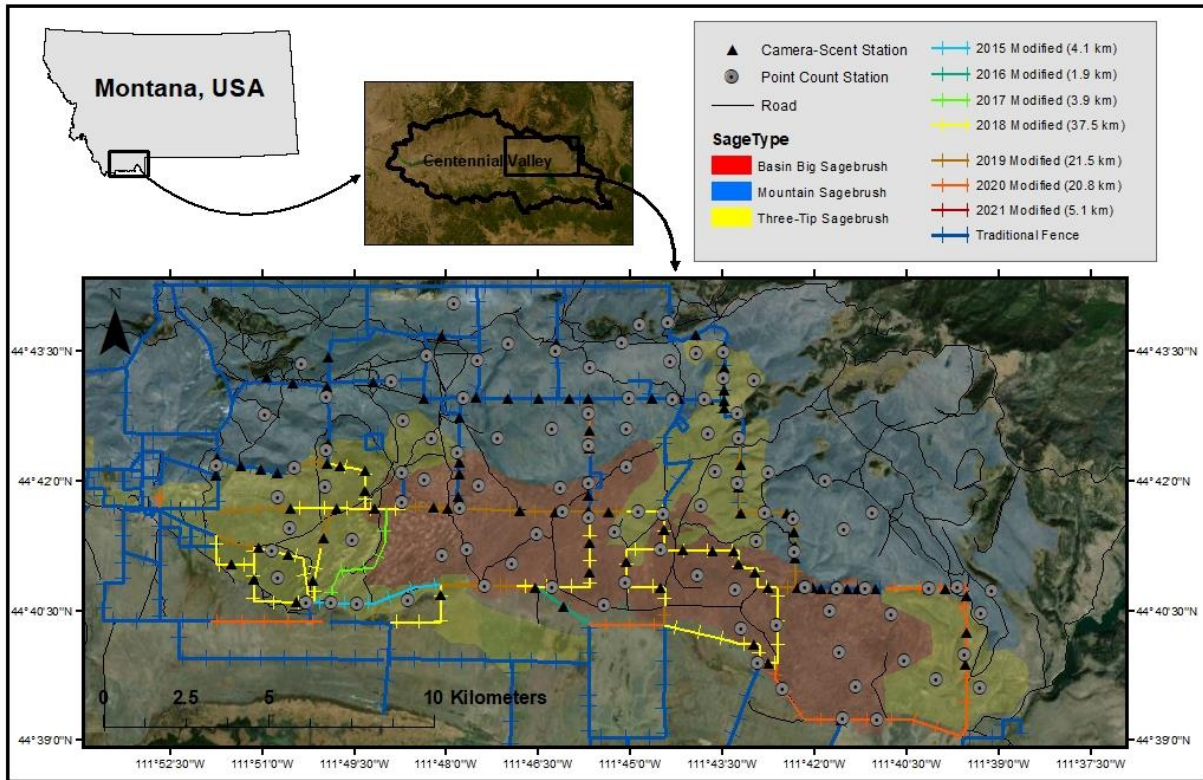


Figure 2-1: A map of the study site showing its location in southwest Montana, USA. Fence lines are color coded on the map to the year they were modified.

Fence Modifications

Approximately 95km of fence modifications were completed in the Sandhills region between the years of 2015-2021. Modifying a fence consisted of raising or removing the lowest wire(s) to implement a 45 cm gap between the ground and lowest wire and adding bundles of sharp metal spikes atop fence posts to inhibit landing by avian predators (perch deterrent; Nixalite®). Minor levels of disturbance were created when installing the modifications on existing fencelines. We consider a traditional fence to comprise all fences not modified with both treatments and consisting of multi-strand barbed or smooth wire, woven wire, or wooden fences.

Predator Monitoring

Ground Predators: Ground predators were monitored during three field seasons (June – August, 2019-21). We randomly generated 100 camera-scent stations across the factors of fence type (modified or traditional) and sagebrush type (BBSA, MTSA, and TTSA) within the sandhills region of the Centennial Valley using ArcGIS10.6.1 (ESRI, Redlands, California, USA; Figure 2-1). A minimum distance of 250m between camera sites was used to promote maximum coverage and site independence according to suggestions from Kays and Slauson, (2008). One passive infrared remote field camera (52 cameras utilized; 28 Browning Strike Force Gen 5 Cameras, 5 Browning Recon Force Advantage Cameras, 10 Moultrie M-990i Cameras, 4 Moultrie D-555i Cameras, 3 Reconyx Hyperfire Cameras, and 2 Uway Vigilant Hunter U150 Cameras; Browning Trail Cameras, Collierville, TN, EBSCO Industries, Inc., Birmingham, AL, Reconyx, Holmen, WI, HCO Outdoor Products, Norcross, GA, respectively) was deployed at each camera-scent station. Cameras were all programmed to take three consecutive photos spaced 1 second apart after each motion trigger, followed by a 1-minute delay period. Each site was sampled for a continuous 21-day period to identify common predators, following the idea that most species will be detected within 14-days but longer periods are needed to capture all species at a site (Moruzzi et al., 2002). We ensured to the best of our abilities that neighboring camera-scent stations were not monitored during the same 21-day period.

Cameras were deployed using rubber gloves and cleaned with alcohol wipes before leaving the site to reduce human scent associated with the station. Cameras were placed in the near proximity of the randomly generated point to find a site with the highest perceived predator use to maximize detections (Lesmeister et al., 2015). Perceived predator use consists of scat near

the fence, well defined paths or tracks, or commonly used fence crossing points. Placement of the camera was on a wooden or metal fence post at a height of roughly 0.5m to ensure capture of our main two target species, badgers and coyotes (Burton et al., 2015). A scent lure (1/32oz of Montana Long Call; Weiser Western Lures, Melrose, MT) was spread upon a bait stick and placed approximately 1m in front of the camera to assist with bringing predators into the cameras field of view (Ferrerias et al., 2018). We didn't expect this to increase a predators use of a site since the visits were not rewarded (Dempsey et al., 2014). We cleared the vegetation between the camera and scent lure to create a clear line of sight for the camera (Burr et al., 2017). Each camera was revisited once per week to collect digitally recorded photographs and re-apply the scent lure, resulting in 3 1-week sampling periods for each 21 day survey.

Avian Predators: We performed point counts during the field seasons of 2019 and 2021. We randomly generated 102 point count stations to monitor avian predators within the study area. To assess objective 1 for the avian predators, 50 point count stations were set to be > 500m from a fence and the additional 52 were located along fences, spread between both modified and traditional fences. These points were also spread across the factor of sagebrush type. To ensure sites along fences and away from fences did not overlap we ensured a 500m minimum distance between stations during sample generation.

We surveyed each point count station three times during the two seasons of study. Each survey consisted of a 10-minute point count and all 102 surveys were completed before moving on to subsequent visits. Our survey methods are based on those described in Ralph et al. (1993), with the corvid survey techniques adopted following those described in Luginbuhl et al. (2001). The corvid survey techniques include longer survey times and a higher wind speed threshold for

being able to conduct the surveys (< 20 kph; Luginbuhl et al., 2001). Our surveys were conducted from sunrise to 1400 hours based on findings that corvid and raptor survey detection rates experience minimal change during this time period (Fuller and Mosher, 1987; Luginbuhl et al., 2001). At the start of each survey, unique identifiers such as station ID and survey date were recorded along with weather variables including cloud cover and wind speed. During surveys, we recorded all avian predators seen, including species from the families Corvidae, Accipitridae, and Falconidae, and estimated their distance from the point count station's center using a handheld range finder.

Statistical Methods

Occupancy Covariates: Covariates used to evaluate ground predator occurrence near fence lines in a grazing dominated landscape included fence type, years since a fence was modified (0-5), distance from other grazing related infrastructure (roads and water tanks), distance from streams, distance from paths, and sagebrush type (MTSA, BBSA, TTSA; Table 3-1). These covariates were selected based on previous research that indicated they may influence predator use of a site through mechanisms such as human provided resource subsidies (Benítez-López et al., 2010; Forman and Alexander, 1998; Lambertucci et al., 2009) or changes in the availability of prey resources (Bylo et al., 2014; Gese et al., 1996; Wilson et al., 2012). We considered elevation as a potential predictor, however sagebrush type is found across a predictable elevation gradient and more informative for our objectives. Information on the locations of fences, roads, and water tanks in the study area were compiled using existing data. Locations and structure types were verified to be accurate through intensive field surveys.

Distance to grazing related infrastructure and streams was measured using ArcGIS10.6.1 (ESRI, Redlands, California, USA). Two additional water sources (a wetland and small pond) were included when calculating stream distance since these are additional natural water sources in the study area. Sagebrush species were visually mapped through detailed field mapping surveys of continuous patches > 0.25 ha that were dominated ($> 50\%$ cover) by a given sagebrush species. Accuracy of these surveys was assessed by Cutting et al. (2019) and high assignment accuracy was found (95.6% accuracy). Google Earth (image date 7/19/2014) was used to quantify distance from the camera locations to the nearest path. We could not differentiate whether a path was created by cattle or other wildlife species, but based on our experience in the study area we believe most of the paths are created by cattle given the evidence of their feces and tracks. Additionally, most paths led to water tanks, fences, and roads used by livestock producers. We predicted that these covariates could influence prey availability and a predator's efficiency at moving throughout the landscape, influencing landscape level patterns in predator use of our study area.

The covariate years since a fence was modified was included to explore the potential for a lag effect in terms of ground predator response to modifications. We predicted that it may take a few seasons for ground predators to consistently recognize the ability to cross a modified fence anywhere and/or create new crossing points. This response is in opposition to using already known crossing-points, since suggestions of crossing site preference has been indicated for multiple species (Zoromski et al., 2022), including many present in our study system.

The same suite of covariates described above was utilized to quantify avian predator occurrence. To address the different life history of avian predators however, instead of distance

from paths we used the covariate distance from trees, since trees provide natural elevated perches on the landscape (Andersson et al., 2009). The covariate years since modification was not included for avian predators since this objective is not attempting to differentiate use between the fence types, rather it is assessing whether having a fence present at a site influences their occurrence. We initially intended to assess avian predator occurrence in relation to each fence type, however our low detection rate and sample size for this predator type did not provide us the power to do so.

Detection Covariates: Since there is the possibility of an animal being present yet going undetected at a survey site, we compiled covariates that may affect the detectability of the species in our study system. For both predator types, we included for detection the covariates of date and sagebrush type (Table 3-1). Date (julian date of when a survey was performed) was included to capture an approximation of the vegetative growth stage throughout a season which could affect the sightability of predators. Sagebrush type was included to accommodate each of sagebrush specie's respective growth forms, with BBSA growing the tallest, influencing how far can be seen in front of each of the cameras and the ability to detect avian predators flying low or on the ground.

For ground predators specifically, we included the two additional covariates of fence type and camera type on their detectability (Table 3-1). We are predominately interested in how fence type influences occurrence rates of ground predators, however we hypothesize that fence type can also influence their detectability. For example, modified fences allow for easier crossing of a fence, improving the likelihood a predator will closely investigate our scent lure and travel within the cameras view angle. We included camera type since we used an array of cameras, and

each camera type has its own functionality. By including camera type as a predictor for species detection, we are attempting to mediate the differences in camera performance inherent with different camera models.

Additional detection covariates for avian predators included time of survey start (minutes after midnight), wind speed, cloud cover, and observer completing the survey (Table 3-1). We predicted that avian predators would be most active earlier in our survey time period (sunrise to 1400) to match the activity patterns of their prey sources. We also predict that with increasing cloud cover and windspeed, the hunting efficiency of these predators will decrease, reducing their activity and subsequently their detectability. We included the observer completing the survey as a covariate since each observer has their own ability to sight and hear avian predators, influencing their ability to detect an individual that is present dependent on its behavior during the survey.

Table 3-1: Predictors used in the occupancy and detection functions in the occupancy analyses of ground and avian predators.

| Variable | Category | Description | Type |
|-------------------------------|--|--|-------------|
| Fence Type ^{*AG} | Occupancy ^{*AG} Detection ^{*G} | Modified or Traditional ^{*G} On fence or Off fence ^{*A} | Binary |
| Sagebrush Type ^{*AG} | Occupancy ^{*AG} Detection ^{*AG} | Dominant sagebrush species at the site | Categorical |
| Year modified ^{*G} | Occupancy | Years since a fence was modified | Continuous |
| Road ^{*AG} | Occupancy | Distance to road | Continuous |
| Tank ^{*AG} | Occupancy | Distance to water tank | Continuous |
| Stream ^{*AG} | Occupancy | Distance to stream | Continuous |
| Path ^{*G} | Occupancy | Distance to path | Continuous |
| Tree ^{*A} | Occupancy | Distance to tree | Continuous |
| Date ^{*AG} | Detection | Ordinal date when survey was started | Continuous |
| Time ^{*A} | Detection | Survey start time | Continuous |
| Cloud cover ^{*A} | Detection | Percent of cloud cover at start of survey | Continuous |
| Wind speed ^{*A} | Detection | Averaged wind speed from start and finish of survey | Continuous |
| Observer ^{*A} | Detection | Observer completing the survey | Categorical |
| Camera Type ^{*G} | Detection | Camera make and model used | Categorical |

*A: Variable used for avian predators

*G: Variable used for ground predators

Occupancy Modeling: To assess the occurrence rates of predators in our study system we utilized occupancy models since they allow the use of detected/not detected data to assess landscape level patterns in habitat use while accounting for imperfect detection (MacKenzie, 2006; MacKenzie et al., 2002). These models incorporate the effects of our covariates on site specific occupancy as well as on the site and survey specific detection process. Our datasets were modeled using the single-season, single species occupancy model of MacKenzie et al. (2002) to estimate differences in the probability of occurrence of our species across our suite of covariates. To fit this model, we used a stacked dataset where each survey site-year combination was considered a distinct site. This approach was utilized since our main focus was on spatial variation in occurrence rather than turnover rates (i.e. colonization and extinction; Crum et al., 2017; Saunders et al., 2019), and our temporal replication was limited. Therefore, our model is a single season occupancy model with year effects included via the additional predictor of year for

both the occupancy and detection processes (Fuller et al., 2016; Linden et al., 2017). This model regards the occupancy status of sites to be independent of one another, conditional on the explicit predictors in the model. We believe this to be a reasonable assumption based on the assessment of our raw predator detections not indicating that a predator occupying a site in year one meant it would also occupy that site in the following years of study.

Prior to running any models, we evaluated pairwise correlations among covariates and found no evidence of high collinearity (Pearson's $r < 0.7$). All our continuous distance covariates were z-standardized to have a mean equal to zero and standard deviation equal to one, allowing comparison of the relative strengths of each of these covariates on the occupancy process (Gutierrez et al., 2017). We modeled the data collected on ground predators by separating badgers and coyotes into their own distinct datasets, as each is expected to interact with their environments differently. We were not able to go to the species level for our avian predators due to low detection rates. Therefore, our avian predator modeling reflects all avian predators encountered during our surveys. We define a site for the ground predators as the area immediately around the camera-scent station. For avian predators, we define the site to be a circle around the point count station with a radius of 250m.

Preliminary analyses for all three datasets produced boundary estimates for the occupancy process when using standard maximum likelihood estimation. We believed this to be a result of the low number of detections made during our sampling efforts, creating a high proportion of 0's (no species detected) to 1's (species detected). Following the preliminary analyses, we chose to implement a ridge regularization to the single species occupancy model as outlined in Hutchinson et al. (2015). This procedure adds a penalty term to the model that

effectively stabilizes the non-intercept parameter estimates by shrinking them towards zero (Hutchinson et al., 2015).

Before running the ridge regularization model for occupancy, we first selected the most appropriate model for the detection function (Gutierrez et al., 2017). To define the detection process, we modeled all the combinations of our detection covariates while holding the occupancy function at its null. We compared these models based on Akaike's information criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson, 2002). We selected the model for detection based on a ΔAIC_c cutoff of 2 and removed models with uninformative parameters from consideration following recommendations by Arnold (2010). All parameters that lent inference to the detection process as selected by AIC_c were included when modelling the occupancy process.

After we selected the detection probability model, we ran the full model with the ridge regularization using a five-fold cross-validation to select the most appropriate penalty term (Hutchinson et al., 2015). We performed diagnostic checks of our models using Dunn-Smyth residuals to identify any instances of lack of fit. Plots of the Dunn-Smyth residuals against fitted occupancy and detection values were constructed using code modified from Warton et al. (2017). Within these plots we searched for trends or strong deviations from zero as indications of lack of fit via a smoother with 95% confidence bands. If the confidence band overlapped zero at any point, there was evidence of lack of fit (Warton et al., 2017).

To calculate standard errors and 95% confidence intervals (*hereafter*: CI) we used parameter estimates computed for 200 bootstrap replicates sampled with replacement from the set of sites (Hutchinson et al., 2015; Moreno and Lele, 2010). We make predictions on how our

covariates affect occurrence probability by holding non-target covariates at their mean value. If a parameter's 95% CI overlapped zero, we concluded that there was not enough evidence in support of an effect on occurrence for said covariate. All analyses were conducted using the statistical program R ((R Core Development Team, 2019), with use of packages 'unmarked' (Fiske and Chandler, 2011) and 'AICcmodavg' (Mazerolle, 2013).

Results

We captured 446 predators on our cameras during 6,331 trap nights. Of those ground predators captured, 221 were of coyotes, 213 were of badgers, and the remaining 12 consisted of long-tailed weasels (*Mustela frenata*; 6), grizzly bears (*Ursos arctos*; 3), gray wolves (*Canis lupus*; 2), and a mountain lion (*Puma concolor*; 1). We re-sampled 16 of the original 900 camera-scent station surveys due to camera malfunctions in the week immediately following the original 21-day survey.

We completed 612 point count surveys across our 102 point count stations throughout the study, during which we made 78 observations of avian predators within 250m of the station center. We detected 30 individuals of the family Corvidae; common ravens (25), black-billed magpies (*Pica hudsonia*; 4), and an American crow (*Corvus brachyrhynchos*; 1). We detected 46 individuals of the family Accipitridae; red-tailed hawks (*Buteo jamaicensis*; 19), northern harriers (*Circus cyaneus*; 16), golden eagles (*Aquila chrysaetos*; 5), Swainson's hawks (*Buteo swainsoni*; 4), and ferruginous hawks (*Buteo regalis*; 2). Lastly, we detected 2 individuals of the family Falconidae; an american kestrel (*Falco sparverius*; 1), and a prairie falcon (*Falco*

mexicanus; 1). We made multiple additional observations, but they fell outside of the site radius and were not included in the analysis.

Badger Occurrence

We detected at least one badger in 167 of the 900 surveys. At the site level, we found 122 out of the 300 distinct site-year combinations where a badger was present. This translates to a naïve occurrence rate of 0.41. Our mean fitted occurrence value for badgers was 0.18, calculated from the average occurrence probability across all sites (0.67) multiplied by the average detection rate (0.27).

We compared 31 models to obtain the most supported model for badger detection probability. There were four models within $2AIC_c$, containing the detection covariates of fence type, sagebrush type, date, and year of survey. The model with sagebrush type and year of survey was equally supported to the model with fence type, sagebrush type, and year of survey by model weight. Since the inclusion of fence type didn't improve the models performance past the penalty of an additional covariate and the CI for fence type overlapped zero, we chose the simpler model. The other two models differed in their inclusion of date or date and fence type. Since the simplest model was nested within the other three and the additional covariates in these models also overlapped zero, we concluded that fence type and date were uninformative parameters and used the detection process modeled on sagebrush type and year of survey when modeling the occupancy process. The sagebrush type BBSA had a negative effect on estimated mean detection probability, decreasing from the reference level of MTSA (0.11 ± 0.06) to (0.03 ± 0.02). The sagebrush type TTSA also had a negative effect on badger detection compared to MTSA, being estimated at 0.06 ± 0.04 . We also noted a negative temporal trend in estimated detection

probabilities across years of our survey, with year 1 at 0.31 ± 0.05 , to year 2 at 0.06 ± 0.01 , and year 3 estimated at 0.06 ± 0.01 .

Occurrence probability appeared positively related to the year a fence was modified, from year 1 to year 2 of surveys, and with increasing distance from roads and streams (Table 3-2). For example, the occurrence probability of badgers increased from a mean of 0.56 ± 0.06 to 0.73 ± 0.06 from zero years since a fence was modified to five years post modification. Probability of occurrence between year 1 and year 2 of surveys increased from 0.77 ± 0.07 to 0.89 ± 0.05 , and in year 3 this probability decreased to 0.53 ± 0.08 . Even though our parameter estimates indicated a positive relationship in occurrence probability with increasing distance from roads and streams, these parameters don't appear informative when assessed across the range of the covariate values. The CIs at either end of the values in the observed dataset for roads and streams showed significant overlap (Figure 3-4a), negating any trend seen within the mean occurrence rates.

We estimated a negative relationship with occurrence probability for the covariates fence type, sagebrush type, distance from water tanks, and distance from paths (Table 3-2). Mean occurrence probability was lower for modified fences (0.54 ± 0.05) than for traditional fences (0.68 ± 0.04). The estimated occurrence probability related to sagebrush type was drastically less for BBSA (0.35 ± 0.06) than for MTSA (0.86 ± 0.04). We didn't detect a significant difference in occupancy probability from our reference level of MTSA for the sagebrush type TTSA (parameter estimate = 0.04, 95% CI: -0.15, 0.22). Distance from water tanks had a strong negative effect on occurrence probability, decreasing from 0.74 ± 0.06 to 0.58 ± 0.06 as the covariate went from its 1% quantile (30m) to the 99% quantile (2290m). The estimated effect of

distance from paths on occurrence probability was similarly strong and decreased from 0.74 ± 0.06 to 0.58 ± 0.06 from the 1% quantile (0.5m) to its 99% quantile (262m) in the observed dataset. We found no evidence of lack of fit for our badger model (Figure 3-2a).

Table 3-2: Results from the ridge regularization occupancy model for badgers. Only showing estimates for covariates with a 95% confidence interval that did not include 0.

| Covariate | Estimate | SE | Lower 95% CI | Upper 95% CI |
|---------------------|----------|------|--------------|--------------|
| Occupancy | | | | |
| Intercept | 1.20 | 0.13 | 0.93 | 1.46 |
| Fence Type | -0.59 | 0.08 | -0.75 | -0.44 |
| Sagebrush Type*BBSA | -1.04 | 0.13 | -1.29 | -0.78 |
| Year Modified | 0.24 | 0.06 | 0.12 | 0.37 |
| Road | 0.12 | 0.03 | 0.07 | 0.18 |
| Tank | -0.25 | 0.04 | -0.33 | -0.16 |
| Stream | 0.10 | 0.03 | 0.04 | 0.17 |
| Path | -0.24 | 0.04 | -0.32 | -0.16 |
| Year* ₂ | 0.41 | 0.07 | 0.27 | 0.56 |
| Year* ₃ | -0.38 | 0.08 | -0.53 | -0.23 |
| Detection | | | | |
| Intercept | -0.18 | 0.02 | -0.21 | -0.14 |
| BBSA | -0.72 | 0.03 | -0.78 | -0.67 |
| TTSA | -0.21 | 0.02 | -0.25 | -0.17 |
| Year 2 | -0.96 | 0.02 | -1.00 | -0.92 |
| Year 3 | -0.66 | 0.03 | -0.71 | -0.61 |

Coyote Occurrence

We detected at least one coyote in 170 of the 900 surveys. At the site level, we found 129 out of the 300 distinct site-year combinations where a coyote was present, resulting in a naïve occurrence rate of 0.43. Our mean fitted occurrence value for coyotes was 0.19, calculated from the average occurrence probability across all sites (0.75) multiplied by the average detection rate (0.25).

We compared 31 different models of the detection process for coyotes. There were two models within $2AIC_c$ containing the covariates date and fence type. The model with date alone was the most supported. Since the inclusion of fence type didn't significantly improve the model and its parameter estimate's CI overlapped zero, we concluded that fence type was uninformative for the detection process of coyotes. We detected a negative temporal trend in estimated detection probability with increasing date (Table 3-3). At the earliest survey start date in our study (June 10th), the estimated detection probability was 0.40 ± 0.01 . This probability decreased as the start date for a survey increased throughout the year to 0.14 ± 0.01 at our latest survey start date (August 8th).

Our estimate of occurrence probability showed a positive trend for the covariates of fence type, sagebrush type, distance from roads, distance from water tanks, and year the survey was completed (Table 3-3). The estimate of occurrence probability for coyotes along modified fences was 0.83 ± 0.01 , whereas for traditional fences it was 0.68 ± 0.02 . We detected an estimated increase in occurrence probability for coyotes in BBSA (0.80 ± 0.02) dominated sites from the reference level of MTSA (0.71 ± 0.03). Sites dominated by TTSA (0.77 ± 0.02) also showed an increase from MTSA. As the covariate distance from road went from the 1% quantile (3m) in the observed dataset to the 99% quantile (1330m), estimated occurrence probability increased from 0.72 ± 0.02 to 0.82 ± 0.02 . Across the same quantiles in the dataset for water tanks (30m – 2290m), we detected an estimated increase from 0.73 ± 0.02 to 0.81 ± 0.02 . The occurrence probability increased throughout the years of our study from 0.71 ± 0.03 in year one, to 0.75 ± 0.02 in year two, and to 0.81 ± 0.02 in year three.

We detected a negative trend in estimated occurrence probability with the covariates distance from streams and years since a fence was modified (Table 3-3). Estimated occurrence probability decreased from 0.82 ± 0.02 to 0.71 ± 0.02 as the covariate distance from streams went from its 1% quantile (0.5m) to its 99% quantile (1710m) in the observed dataset. The occurrence probability for fences not modified or modified that year (year modified = 0) was 0.82 ± 0.02 and decreased to 0.65 ± 0.02 for a fence modified 5 years prior to a survey being conducted. We did not detect an effect of distance from path on the occurrence probability of coyotes (parameter estimate = 0.03, 95% CI: -0.02, 0.07). We found no evidence for lack of fit in our coyote model (Figure 3-2b).

Table 3-3: Results from the ridge regularization occupancy model for coyotes. Only showing estimates for covariates with a 95% confidence interval that did not include 0.

| Covariate | Estimate | SE | Lower 95% CI | Upper 95% CI |
|----------------------------------|----------|------|--------------|--------------|
| Occupancy | | | | |
| Intercept | 0.69 | 0.06 | 0.57 | 0.81 |
| Fence Type | 0.75 | 0.13 | 0.49 | 1.00 |
| Sagebrush Type* _{BBSA} | 0.30 | 0.07 | 0.16 | 0.43 |
| Sagebrush Type* _{T TSA} | 0.15 | 0.04 | 0.06 | 0.24 |
| Year Modified | -0.22 | 0.07 | -0.35 | -0.09 |
| Road | 0.17 | 0.03 | 0.12 | 0.23 |
| Tank | 0.14 | 0.02 | 0.09 | 0.18 |
| Stream | -0.17 | 0.02 | -0.22 | -0.13 |
| Year* ₂ | 0.14 | 0.07 | 0.00 | 0.28 |
| Year* ₃ | 0.18 | 0.08 | 0.03 | 0.34 |
| Detection | | | | |
| Intercept | -1.14 | 0.01 | -1.15 | -1.12 |
| Date | -0.42 | 0.01 | -0.43 | -0.41 |

Avian Predator Occurrence

We detected at least one avian predator in 75 of our 612 point count surveys. At the site level we found an avian predator present at 66 out of 204 distinct site-year combinations, resulting in a naïve occurrence rate of 0.32. Our average fitted occurrence value across all sites was 0.12, calculated from the average occurrence probability (0.80) multiplied by the average detection rate (0.15).

We compared 127 models to identify the most supported model of the detection process for avian predators. There were six models within $2AIC_c$ of the most supported model which included the covariates cloud cover and sage type. Four of the six models only varied in their inclusion of one covariate; date, year a survey was completed, wind speed, and observer. Since these models didn't overcome the penalty associated with an additional parameter and the additional parameter's CI overlapped zero, we concluded these parameters were most likely uninformative and removed them from our consideration. The other two models within $2AIC_c$ included the combinations of date and year a survey was completed, and date and wind speed. While these models were within the cutoff range, both additional parameters in both combinations had 95% CIs that overlapped 0, resulting in those models being removed from consideration as well. Therefore, our most supported model for the detection process included a positive trend with increasing cloud cover and a negative trend with sagebrush type from the reference level of MTSA (0.19 ± 0.01). At 0% cloud cover, the estimated detection probability was 0.04 ± 0.01 , and increased to 0.20 ± 0.01 at 100% cloud cover. Estimated detection probability in BBSA dominated sites was 0.06 ± 0.01 and in TTSA dominated sites was 0.07 ± 0.01 .

We did not find support for an effect of fence type (on or off fence) on occurrence probability for avian predators (parameter estimate = -0.23, 95% CI: -0.49, 0.03). We also did not find support of an effect on occurrence probability considering the covariates distance from water tanks (parameter estimate = 0.10, 95% CI: -0.01, 0.20) or distance from trees (parameter estimate = -0.07, 95% CI: -0.23, 0.08). There was no evidence of a difference in occurrence probability for MTSA dominated sites to sites dominated by TTSA (parameter estimate = 0.12, 95% CI: -0.20, 0.45) or for a difference between years (year two parameter estimate = -0.17, 95% CI: -0.39, 0.04).

We found support for a negative trend in estimated occurrence in relation to distance from roads and distance from streams (Table 3-4). As the covariate distance from roads increased from its 1% quantile (2m) in the observed dataset to its 99% quantile (1495m), the estimated occurrence probability decreased from 0.92 ± 0.03 to 0.61 ± 0.03 . Across this same quantile range in the observed dataset for distance from stream (5m-1745m), the estimated occurrence probability decreased from 0.88 ± 0.03 to 0.70 ± 0.03 . We also detected a negative effect on occurrence probability for sites dominated by BBSA (0.68 ± 0.02) from sites dominated by MTSA (0.87 ± 0.01). We found no evidence for lack of fit in our avian predators model (Figure 3-2c).

Table 3-4: Results from the ridge regularization occupancy model for avian predators. Only showing estimates for covariates with a 95% confidence interval that did not include 0.

| Covariate | Estimate | SE | Lower 95% CI | Upper 95% CI |
|---------------------|----------|------|--------------|--------------|
| Occupancy | | | | |
| Intercept | 1.86 | 0.21 | 1.44 | 2.28 |
| Sagebrush Type*BBSA | -0.54 | 0.15 | -0.84 | -0.24 |
| Road | -0.61 | 0.07 | -0.75 | -0.48 |
| Stream | -0.34 | 0.05 | -0.45 | -0.24 |
| Detection | | | | |
| Intercept | -1.47 | 0.02 | -1.50 | -1.44 |
| Cloud cover | 0.41 | 0.01 | 0.39 | 0.43 |
| Sagebrush Type*BBSA | -0.60 | 0.03 | -0.65 | -0.55 |
| Sagebrush Type*TTSA | -0.38 | 0.02 | -0.42 | -0.33 |

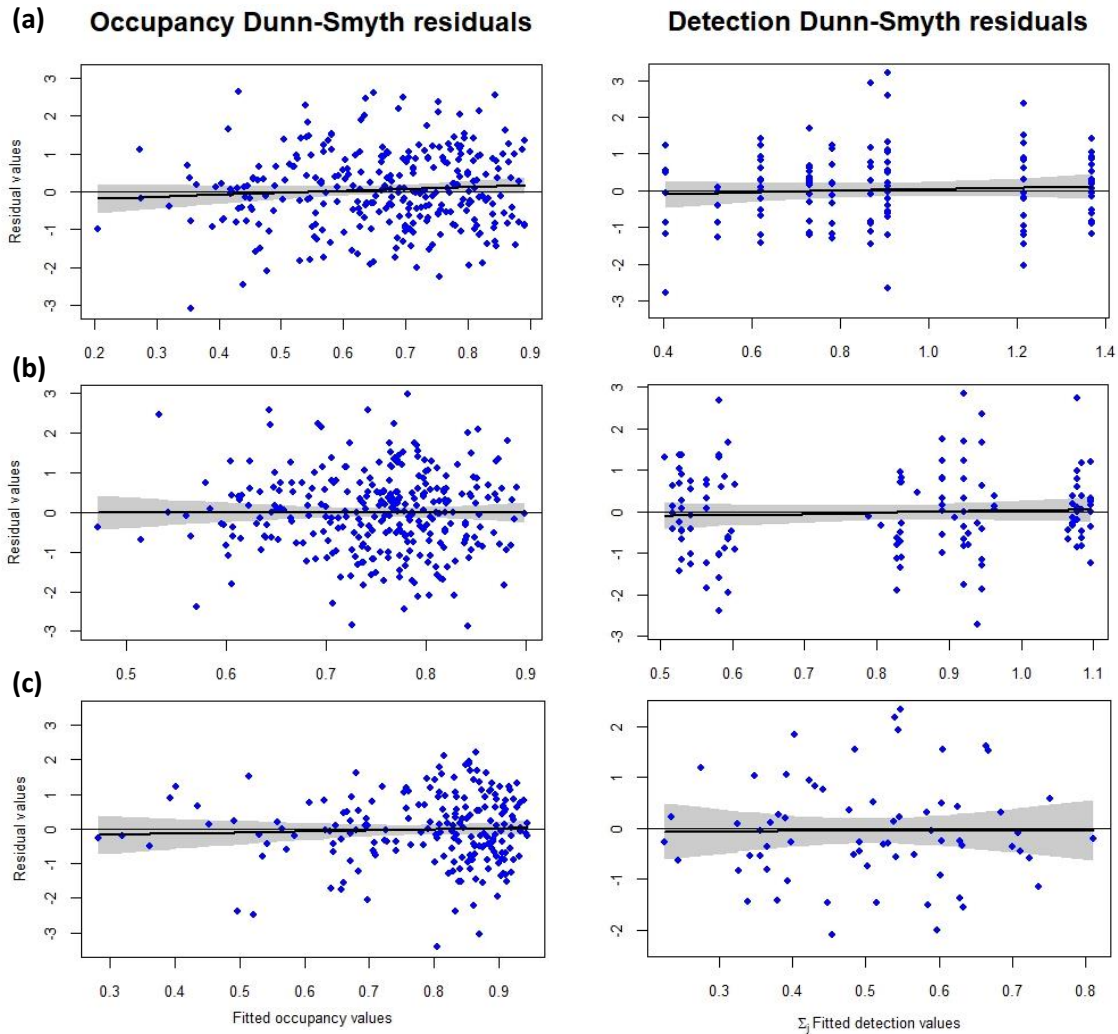


Figure 3-2: Dunn-Smyth residuals plotted against fitted occupancy and detection values for badgers (a), coyotes (b), and avian predators (c). The distinct groupings of detection residuals in badgers and coyotes are due to categorical covariates modeled for badgers and the relative spread of survey start dates for coyotes.

Discussion

Predator Detectability

In studies of animal occupancy, detection is a driving factor in one's ability to relate occurrence to covariates (MacKenzie, 2006). We noticed relatively low detection rates across all three groupings of species we modeled (badgers = 0.27, coyotes = 0.25, and avian predators =

0.15). The low detection for ground predators could be due to an acclimation to the scent lure throughout the season (Burr et al., 2017). This could cause the results seen with decreasing detection rates seen across years in badgers and across survey start date in coyotes, suggesting coyotes may become acclimated to our scent lures within a season whereas badgers may experience this across years. Another explanation could be attributed to human avoidance, considering coyotes tend to avoid areas with high human presence (Magle et al., 2014). We attempted to mask our presence at the camera-scent stations, however the repeat visits and presence of the foreign object (the camera) may reduce occurrence in an area after it has been discovered. We noticed multiple coyote photographs where it was clear the animal had detected the camera and a previous study has shown coyotes tend to be wary of these sorts of survey methods (Sequin et al., 2003). The low detection of avian predators is likely due to a combination of the relatively low densities of raptors and their ability to range over large areas (Newton, 1979). Even though a site may be utilized by an avian predator, our ten-minute time limit for the survey may have precluded detecting them at the site. On multiple occasions an avian predator was observed within 250m of the site within five minutes of the start or end of the survey. Our study site is also characterized by many small rolling hills, causing visibility at the ground level to not be uniform across all areas of our point count station. We did our best to mediate this by moving within the point by up to 30m to find higher ground for better visibility of the whole site.

A notable result in the detection process that did not fall in line with our prediction was the increase in estimated detection with increasing cloud cover for avian predators. Our initial inclination was that increasing cloud cover would create a situation where the flatter light would

cause prey to be harder to detect for avian predators, reducing their activity and subsequently our ability to detect them. While this lowered hunting efficiency may still be reducing their activity levels, the reason we see increases in detectability is related to how most of our avian predators were observed. The majority of our detections were made when the predators were flying (83%), often above the horizon line of the many rolling hills at the study site. With increasing cloud cover avian predators above the horizon line have been shown to be easier to detect whereas detection decreases for predators flying at lower altitudes (Nolte et al., 2016). This relationship likely would not have been as strong if our avian predators were detected more frequently flying low or on the ground.

Predator Occurrence

Previously, fences have been shown to facilitate predator movement and hunting efficiencies (Coates et al., 2016; Hovick et al., 2014), yet we have encountered no studies that have attempted to alter this behavior by experimentally modifying these structures. Higher use of fences by predators can have cascading impacts on the prey communities they utilize. Our modeling approach highlights the importance of this change in fence structure, along with other landscape variables on probability of predator occurrence throughout the landscape. Both coyotes and badgers showed evidence of an effect of fence modifications on their occurrence at our sites. We did not, however, find support for higher use of sites with a fence present for avian predators. We observed that the dominant sagebrush species in an area can impact a predator's use of the landscape. We also observed multiple effects of other linear and point features present at the site on occurrence of predator species. Our results showing different responses in

occurrence by predator species to the landscape features highlight how predation risk can change throughout an area.

Our results regarding fence type indicate that both badgers and coyotes respond differently to the modifications. We observed an overall decrease in occurrence rates along modified fences for badgers. This relationship however loses strength with time, suggesting badgers may be responding more to the disturbance associated with modifying fences than to the improved permeability the modifications facilitate (Figure 3-3a). Since the study site is dominated by sagebrush, when modifications were performed there was inevitable machine trampling and destruction of the brush species within 5m of the fence. This makes travel and visibility for low to the ground species more difficult due to the increase in large woody debris across the commonly used travel paths. For species such as badgers, shorter and less dense vegetation acts to increase their perceptual range (Zollner and Lima, 1997), whereas the addition of the trampled brush would have the opposite effect. The higher perceived occurrence rates of badgers the closer a path was to a site bolsters this idea due to the high amount of paths running along fence lines. As livestock and other wildlife species utilize these same paths, the debris will slowly decrease and be moved out of the preferred travel pathways, providing a possible explanation for the increase in occurrence along modified fences in the years post modification. Coyotes, on the other hand, show a higher occurrence along fences modified recently. This response then decreases to the estimated occurrence along traditional fences up to five years after the fence was modified (Figure 3-3b). Generally speaking, coyotes often show net gains in functional responses to anthropogenically caused landscape change (Heim et al., 2019), suggesting their higher occurrence along recently modified fences may be in response to this

recent disturbance. Additionally, the debris that may be hindering badger travel would have less effect on a coyote due to their differences in height and stature. Since the debris will have a minimal effect, the reduction in sagebrush density following a modification may facilitate their travel along fences in an even greater capacity. The vegetative structure will trend towards pre-disturbance levels in the years following the modifications, resulting in the temporary increase in mobility possible along modified fences to likely be diminished 5 years post modification.

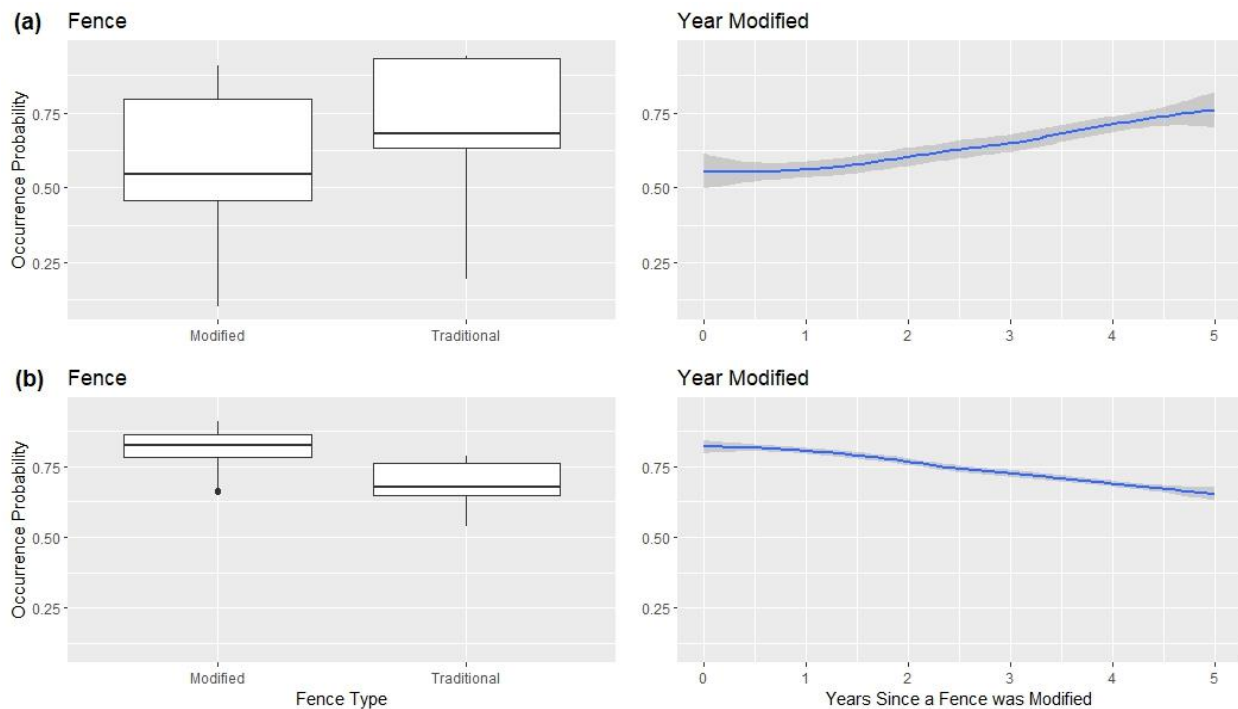


Figure 3-3: Plots of estimated occurrence rates against fence type and year modified for badgers (a) and coyotes (b). The lines represent the mean estimates and the shaded areas around the lines represent the 95% CIs.

We detected notable differences in occurrence with other infrastructure related to livestock operations in our predators in complement to the effect of fences on ground predators. We found that coyotes appear to have lower occurrence rates in closer proximity to roads and

water tanks (Figure 3-4b), a result that is consistent with previous studies (Sunga et al., 2017; Wilson et al., 2012). The Centennial Valley has a minimal amount of human presence, creating a more natural system. Predators such as coyotes in this system will be less habituated to human presence than coyotes in the surrounding vicinity of a city, potentially raising their wariness of humans on the landscape. Since roads and cattle tanks are some of the highest frequented areas by people at our study site, we believe the lower occurrence rates near roads and water tanks may be attributed to human avoidance. Badgers showed the same trend with roads as coyotes, albeit much weaker (Figure 3-4a). Since smaller mammals such as badgers tend to have reduced home range sizes compared to that of larger mammals such as coyotes, they are likely to be less sensitive to infrastructure developments (Benítez-López et al., 2010; Buskirk, 2004; Harestad and Bunnell, 1979). We did detect a different trend with badgers in regards to water tanks however, in that we found higher occurrence probabilities nearer to water tanks (Figure 3-4a). This result is likely due to availability of prey, as badgers are more driven by prey availability than vegetation structure or composition when selecting habitats (Eldridge, 2004; Lindzey, 2003). The primary prey of badgers is generally the dominant burrowing rodent in an area (Goodrich and Buskirk, 1998; Messick and Hornocker, 1981), which at our site is ground squirrels (*Urocitellus spp.*). Ground squirrels have been shown to be positively affected in terms of abundance by increased grazing intensities that reduce the vegetation biomass and height (Bylo et al., 2014; Schieltz and Rubenstein, 2016). At our site, water can be limiting depending on the pasture in use. In areas where water is limiting livestock will generally focus their grazing closer to water tanks (Ganskopp, 2001). The higher grazing intensity near water tanks will create better predator visibility habitat for ground squirrels, and since prey is the driving factor in

badger habitat selection it is not surprising to see increasing occurrence rates nearer to water tanks at our site. Badgers may also experience improved mobility near water tanks since most paths in our study area proliferate around these structures and we see the increase in badger occurrence with proximity to these paths.

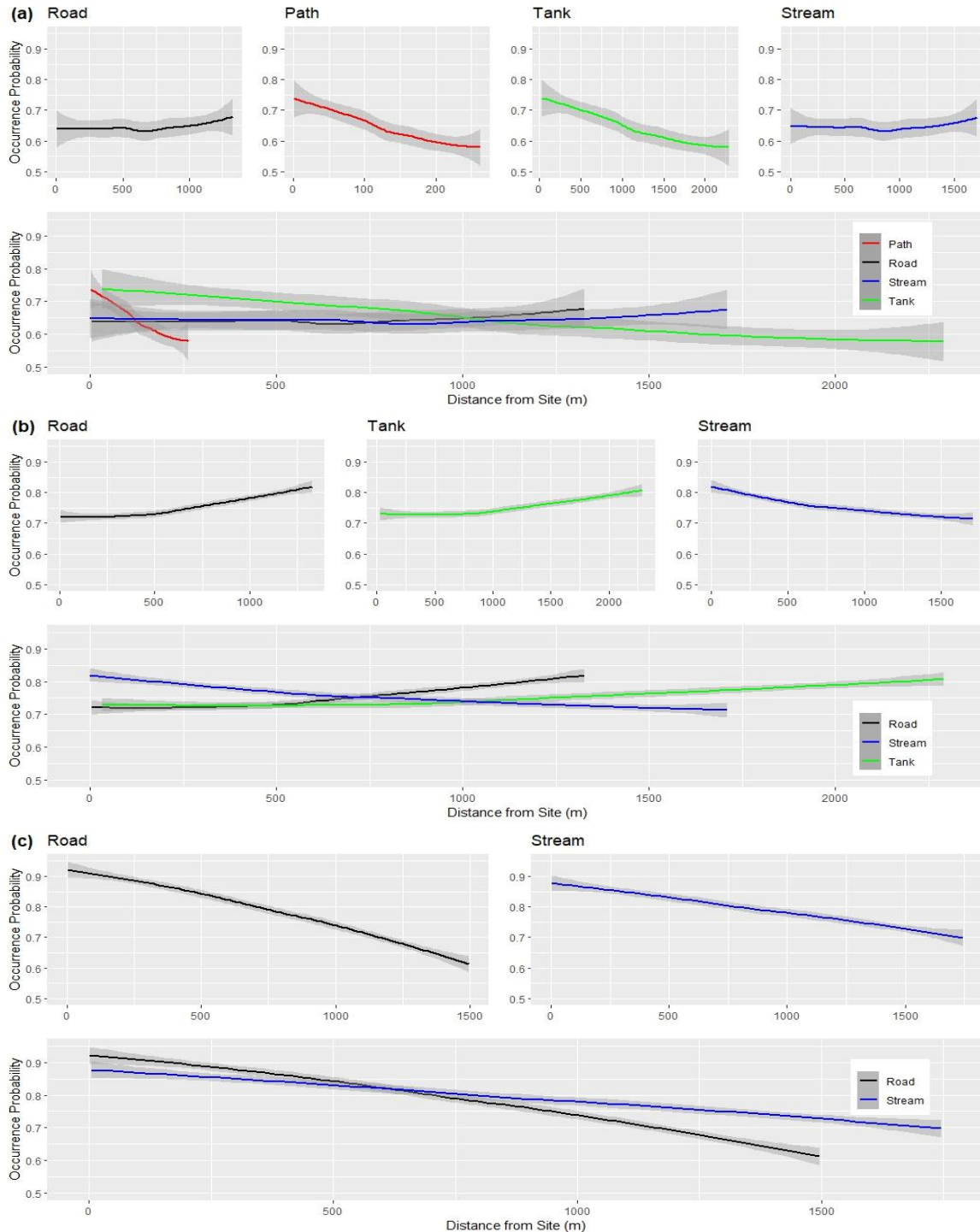


Figure 3-4: Plots showing occurrence rates against linear distance covariates for badgers (a), coyotes (b), and avian predators (c). For each species set, the top row shows plot of single variables across their respective distances in the observed dataset, the bottom plot of each set shows each covariates effect relative to the covariate with the greatest distance range. The lines represent the mean estimates and the shaded areas around the lines represent the 95% CIs.

Only one infrastructure component appeared to affect avian predator occurrence, the proximity to roads. Avian predators appear to occur at higher rates the closer they are to roads (Figure 3-4c). A fair amount of roadkill in the form of small prey species occurs throughout the study site, and the majority of predators seen utilizing this anthropogenic subsidy were avian (O’Harra; personal observation). Previous studies have documented the use of roadkill by avian predators as well (Forman and Alexander, 1998; Lambertucci et al., 2009). This observation suggests that avian predators may utilize road corridors more so than ground predators. The increased open ground and reduced vegetation near roads may also have the impact of improving an avian predator’s hunting abilities by improving their visibility of ground dwelling prey (Benítez-López et al., 2010; Bui et al., 2010).

Natural sources of water, i.e. streams, also appear to have an effect on predator occurrence. We detected negative trends in occurrence for both coyotes and avian predators in relation to their distance from streams (Figure 3-4b & 3-4c). In high elevation sagebrush steppe habitats, the mesic meadows associated with streams can be important refugia for many prey species that rely on a high diversity of forbs and insects for food resources. Since both coyotes and avian predators are highly mobile, it is probable that they will travel further to utilize sites that provide better prey availability, such as these areas nearer to streams. Additionally, coyotes have been found to have higher predation rates at these wetter sites, presumably because prey populations congregate in these areas (Gese et al., 1996). Badgers on the other hand showed a weak positive trend in their occurrence in relation to distance from streams (Figure 3-4a). This may be due to their smaller home range size and lower mobility as previously discussed with

their proximity to roads. Badgers may not have the ability to travel to these sites of prey refugia as easily as coyotes and avian predators.

The dominant sagebrush species at a given site appear to be a main effect in which predators will occur more frequently there. In BBSA, both badgers and avian predators have lower estimated occurrence than sites dominated by MTSA or TTSA (Figure 3-5a & 3-5c). BBSA doesn't support as robust of undergrowth vegetation as seen in our other two sagebrush types (Davies and Bates, 2010; Schroff et al., 2018). This reduction in cover at the ground level may be limiting for a badger's main prey species of ground squirrels in that they do not have adequate cover to hide from predators (Bylo et al., 2014), and therefore will likely occur in lower abundances at these sites. Since badgers' main driver of habitat selection is prey availability, the idea of lower numbers of prey in BBSA is a reasonable explanation as to their lower estimated occurrence at these sites. The lower occurrence of avian predators is not surprising either given how much the more tree-like growth form of BBSA will restrict their visibility compared to MTSA and TTSA. Out of the two species of big sagebrush (*Artemisia tridentata* spp.), BBSA generally grows taller (148cm average) and has a wider crown (193cm average) than MTSA (96cm in average height and 153cm in average crown diameter; McArthur and Welch, 1982). TTSA is a smaller sagebrush species and generally grows 20-80cm in height, with a smaller crown than big sagebrush species (Lesica, 2012). Coyotes on the other hand showed higher occurrence rates in BBSA compared to the other two sagebrush types in our study area (Figure 3-5b). With our other two predator types showing lower occurrence in these areas, it is feasible that coyotes are filling a niche space. The higher mobility of coyotes over badgers also allows for better access into the larger expanses of BBSA dominated sites in the southern portion of our

study area (Figure 3-1). The taller growth form of BBSA paired with less lower lateral cover (McArthur, 1979; Schroff et al., 2018) may act to increase a coyote's sight and mobility in relation to the other sagebrush types. We also noted a slightly higher occurrence rate for coyotes in sites dominated by TTSA over those of MTSA. This could again come down to the stature differences between the sagebrush species. The lower average height of TTSA means that in many cases a coyote would have better visibility in TTSA dominated sites by allowing them to more frequently see above the sagebrush, improving their ability to detect prey.

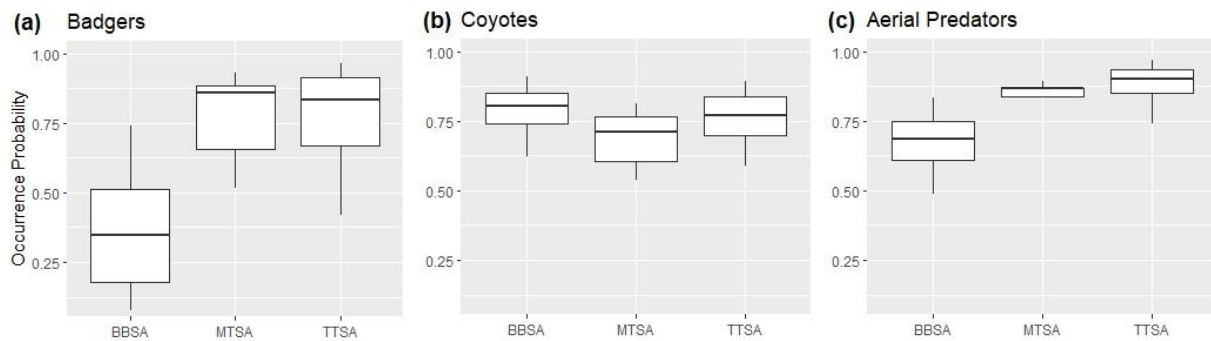


Figure 3-5: Box plots showing the relationship between occurrence probability and sagebrush type for badgers (a), coyotes (b), and avian predators (c). The sagebrush species is shown on the x axis.

The strongest relationships seen in our distance covariates for badgers was the effect of distance from water tanks and distance from paths. The distance from water tanks had a slightly larger negative effect on occurrence than paths, yet this relationship was carried over a much wider area (Figure 3-4a; bottom panel). The high impact of distance from paths over a smaller range (~200m) indicates this may be a driving factor in badger use of our study site. This could mean that ease of mobility along with prey availability drives how badgers utilize our study site. For coyotes, we see both distance from roads and distance from streams having the greatest

effect on occurrence of our distance covariates. Human avoidance coupled with prey availability may be the driving factors for coyote occurrence throughout the study site. Lastly, for avian predators we see the greatest effect on occurrence with the covariate distance from roads. This large estimated effect size coupled with the same trend in distance from streams suggests that prey availability is a driving factor of avian predator use of the study site, with higher preference given to areas where human subsidies are present and prey visibility is greater.

Predators and Sage-Grouse

Our results lend inference as to which predators may be responsible for sage-grouse nest predations across the complex landscape of the Centennial Valley. Sage-grouse have shown responses in previous studies to many of the same covariates we assessed for our predator occurrence rates. For instance, sage-grouse have been shown to select nest sites where there are lower densities of avian predators (Dinkins et al., 2012). At our study site, the areas with the lowest occurrence of avian predators were further from roads and streams (Figure 3-4c). In other study systems, sage-grouse have been shown to avoid areas near roads (Aldridge and Boyce, 2007; Dinkins et al., 2014) and riparian areas (Dinkins et al., 2014; Doherty et al., 2010) when selecting nesting habitat. This selection preference coupled with where we estimated higher occurrence rates of avian predators supports the idea that sage-grouse select nest sites that hide their nests from visual predators but not olfactory predators (Conover et al., 2010).

Badgers and coyotes have the ability to use olfactory cues when hunting, with badgers specifically relying on smell more than visual cues due to their relatively poor eyesight (Messick et al., 1981; Minta, 1993). Hunting associations have been documented between badgers and coyotes (Minta et al., 1992; Thornton et al., 2018), but we do not believe this to be a common

occurrence at our study site. We did not detect any badgers and coyotes in the same or subsequent photographs and no detections of either species were followed with the detection of the other within five hours. Additionally, estimated occurrence rates in regards to our covariates showed marked differences in response for these two predators. At sites in close proximity to water tanks, badgers are the only predator we assessed that shows evidence for increased occurrence. Coyotes appear to avoid water tanks, whereas avian predators showed no evidence of an effect. Sage-grouse that nest near water tanks are therefore more likely to be at higher risk of predation from badgers. We also noticed the similar responses of coyotes to that of avian predators in regards to distance from streams. Both those predator types showed estimated increases in occurrence the closer they are to streams. Even though sage-grouse tend to avoid nesting near streams, research has indicated that at some sites they will use these wetter sites when brood-rearing (Dinkins et al., 2014). Wetter sites along streams in general are riskier habitat for prey species since these sites often contain a greater number of predators (Wilcove, 1985). The predators that appear to be utilizing streams more often in our study site are avian and coyotes.

Cutting et al. (2019) showed that sage-grouse nesting near fences have much lower survival than nests located greater than 100m away. Our modifications to fences attempted to lower the predator occurrence rates along this infrastructure type. The variable results seen in coyotes and badgers indicate that predator specific predation risk may change in the years following modifications. This change is important when considering modifying fences for prey species survival. In the same study, Cutting et al. (2019) showed that sage-grouse nests in BBSA dominated sites had much lower survival probabilities than in MTSA or TTSA. Given that only

coyotes had a higher occurrence rate at these sites, it is likely that they are a main factor in nest predations in BBSA. Badgers showed the lowest estimated occurrence rates in BBSA, indicating that relative predation risk from badgers may be low in these areas. By comparing studies of sage-grouse nest success and occurrence rates of their common nest predators, it is possible to speculate the relative predation risks associated with landscape variables.

Conclusion

Fences continue to proliferate with greater than one million kilometers of fence already present across the American West (McInturff et al., 2020). Both avian and ground predators have been shown to utilize fences along with other infrastructure types for the facilitated mobility and hunting efficiencies they provide. Our results indicate that different predator species respond differently to fences. Our modifications produced variable results dependent on the species being assessed. Differing responses by predators to this management action has the potential to impact prey species in various ways. Understanding predator-prey dynamics in relation to natural and anthropogenic features of the landscape is critical for managers when considering potential management actions. Further research of our novel fence modification as a management action to increase prey survival by altering predator behavior should consider a wider suite of predators and how those predators interact with one another and their shared prey resources.

CHAPTER FOUR

CONCLUSIONS

In sagebrush steppe ecosystems there are many different natural and anthropogenic features that influence predator-prey dynamics. Throughout my study I have assessed three different predator types (badgers, coyotes, and avian) and one of their shared prey resources (sage-grouse). I have shown that these predators and prey have their own responses in magnitude and direction to an array of features at my study site. I observed that badgers, coyotes, and sage-grouse all showed a response to the experimental modification of fences. Badger occurrence decreased near recently modified fences, whereas coyote occurrence increased along these same structures. Nest survival of sage-grouse near modified fences was increased compared to traditional fences and that response changed in magnitude in relation to other landscape features. The results from both chapters indicate that specific predators' occurrence rates influence the predation risk for sage-grouse nests differently throughout the landscape.

Even though sage-grouse generally select nest sites away from major roads (Aldridge and Boyce, 2007; Dinkins et al., 2014) and experience higher nest survival in these areas (Naugle et al., 2011), proximity to 2-track roads does not appear to have an effect on sage-grouse nest survival or selection (Smith et al., 2018a). In Chapter Two, I found no evidence for an effect of distance to roads on nest survival. The roads at our study site have low levels of traffic, are mostly unpaved 2-tracks, and are generally used for access by livestock operators during the sage-grouse nesting season. I found a strong increase in avian predator occurrence near roads, slight evidence for an increase in badger occurrence, and a decrease in coyote occurrence. This

indicates that nests in areas closer to roads are likely subject to higher predation risk from avian predators over ground predators. Finding no effect of roads on nest survival, however, indicates that avian predators may not be the dominant nest predators at my study site. This idea is supported since the average distance of nests from a road was 274m, well within the 1km effect size of major roads that have been found to reduce nest survival (Naugle et al., 2011).

My results from Chapter Three show that both badgers' and coyotes' occurrence rates may be affected by proximity to water tanks, but I found no evidence for an effect on avian predator occurrence. Badgers show a strong increase in occurrence nearer to water tanks and coyotes showed the opposite effect. In Chapter Two I found no effect of proximity to water tanks on nest survival of sage-grouse. Sage-grouse have been shown to select nest sites away from anthropogenic structures (Dinkins et al., 2012), providing a reasonable explanation as to why badger predation on nests at my study site may be low since their occurrence is positively associated with distance to water tanks and the paths often associated with them. The average distance from a nest to a water tank was 823m, indicating grouse may be showing some avoidance of water tanks in the study area.

I found higher nest survival associated with areas with greater wetness potential (higher CTI values; slope and upstream contributing area), which at my study site is the mesic meadows associated with streams. The increased wetness areas have potential for more robust vegetation growth, providing greater cover for nests in these areas. Both coyotes and avian predators showed evidence for increased occurrence closer to these wetter sites, likely from the increased abundance of prey (Gese et al., 1996). The increase in nest survival found with wetter sites may be due to a combination of better nest concealment cover and an abundance of alternative prey.

Additionally, even though nest survival was higher at wetter sites, the average CTI value for a nest was 8 in a range from 5 (driest observed nest site) to 17 (wettest observed nest site). This indicates that sage-grouse may not perceive these areas as better nesting sites even with the increase in nest survival I detected. When selecting nest sites, sage-grouse have shown an avoidance of wetter areas (Dinkins et al., 2014; Doherty et al., 2010), which I believe may be occurring at my study site as well (average distance from a stream was 578m). Combining this idea and the fact that streams were the only landscape feature aside from roads I found to have evidence of a positive effect on avian predator occurrence, it is unlikely avian predators are a main cause of nest failure at my study site.

My results of nest survival in relation to sagebrush type (using elevation as a proxy) corroborate the results found by Cutting et al. (2019) that showed lower survival for the lower elevation BBSA sites. This result also implies that avian predators may not be the dominant nest predators in our study system since their estimated occurrence was much lower in BBSA dominated sites. The visual obstruction by large sagebrush is generally greater in these areas (McArthur and Welch, 1982), preventing efficient hunting by avian predators. With lower nest survival at these sites and only coyotes showing an estimated increase in occurrence, it is likely that coyotes are the dominant nest predator in BBSA stands in the study area. Coyotes are also the only predator I assessed that showed any evidence for an increase in occurrence in TTSA over the rates in MTSA, indicating predation risk from coyotes may be higher at these sites as well.

Experimental modification of the fences did appear to increase the DNS for sage-grouse. This effect of modified fences on nest survival held for all 8 years that we monitored sage-grouse

nests. Coyotes and badgers both showed similar occurrence probabilities along traditional fences, yet there was evidence for an increase in occurrence probability for coyotes and a decrease for badgers along modified fences. For both these species however, their occurrence probabilities along modified fences returned to rates seen along traditional fences within 5 years of the modifications being installed. This indicates that these predators may be responding more to the disturbance associated with installing modifications rather than the actual treatment. The disturbance associated with installing fence modifications may have temporarily increased coyote predation risk while decreasing the risk from badgers. Since coyotes and badgers have similar occurrence probabilities along traditional fences and modified fences after 5 years, it is likely that neither predator dominates the predation events close to fences. Instead, the lower nest survival near fences is likely due to the general increase in predator usage of linear features, causing higher chances for opportunistic encounters with a sage-grouse nest.

I also found evidence that the effectiveness of fence modifications at improving nest survival increased with increasing elevation and wetter sites. Higher elevation sites are mostly dominated by MTSA stands, which generally have greater vegetative species richness and diversity (Davies and Bates, 2010), the same effect seen in areas near streams. The potential for higher abundances of prey associated with this type of site combined with the reduced barrier effects associated with modified fences may act to reduce a predators search rate for nests. The greater concealment offered at these sites will also make nests harder to detect, and with abundant alternative prey it is unlikely predators are focusing on nests as their main food source in these areas. More fences were modified in the lower elevation sites however, and the greater number of nests found in these areas may be the reason for these results.

Overall, it appears that the highest predation risk for sage-grouse nests when considering the range of covariates we assessed comes from coyotes. Coyotes showed the most similar avoidance pattern to anthropogenic features as documented with sage-grouse nests (i.e. roads and water tanks). Out of the predators I assessed they were also the only predator to show higher occurrence in both sagebrush types with lower estimated sage-grouse nest survival (BBSA and TTSA; Cutting et al. 2019). Within 100m of a fence however (~20% of the study site), it appears that no single predator is more responsible for the lower observed nest survival rates. Instead, the increased usage of linear features by multiple predator types may act to make areas near fences riskier nesting habitat in general. After relating avian occurrence and nest survival to the landscape features I assessed, it does not appear that avian predators when considered as a group are a driving factor in predation risk at my study site. However, this may be a result of the low sample size and detection rates seen along with too few of observations of each species to model occurrence rates at the species level.

Future studies of this novel management technique could benefit from a longer study duration (> 10 years) since we detected a lag effect on how modifications affected ground predator occurrence. It is important to know if this is just a short-term gain in nest survival near modified fence or if the increase in survival persists. Additionally, placing cameras on the actual nests to document predation events could reveal the true predators of nests at a site. Right now we are limited to speculation based on predator occurrence rates and estimated nest survival in relation to the same covariates. Since cameras on the nests is logistically challenging one could instead include a wider suite of predators being assessed for. Other species such as red foxes (*Vulpes vulpes*), bobcats (*Lynx rufus*), and even elk (*Cervus canadensis*; Conover and Roberts

2017) have also been documented predated sage-grouse nests, just at lower rates than the main three I chose to assess in this study. Assessing this management technique for other prey species demographics is also an important consideration. Improving survival of one part of a species life history may impact other stages, and even other species. More research will need to be done in order to better understand how modifying fences can be used as a tactic to improve prey species survival. Overall, the promising result of Chapter Two showing evidence for an increase in nest survival near modified fences promotes this as a viable management tactic to improve nest survival of a ground dwelling bird species.

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