Effects of Livestock Grazing and Habitat on Predator-Specific Nest Mortality and Spatiotemporal Activity Patterns of Sage-Grouse Nest Predators

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Abstract

Quantifying how anthropogenic land use affects wildlife communities is critically important for balancing socioeconomic activities with wildlife conservation and management. Wildlife often perceive human activity as a risk and respond by increasing anti-predator behaviors (e.g., vigilance or fleeing) and/or partitioning themselves in space or time. Alternatively, some species may be drawn to human activities and benefit from anthropogenic subsidies such as food, water, or habitat features. Regardless, shifts in animal behavior and spatiotemporal activity patterns can alter key ecological processes that help maintain wildlife communities. For example, human activities can impact predator-prey interactions by altering spatiotemporal overlap of predators and prey or by altering predator foraging efficiency. Predation can shape the structure and function of wildlife communities and regulate prey populations via top-down processes. Thus, quantifying how human activities influence predator-prey interactions enhances our ability to make well-informed decisions regarding wildlife management. However, quantifying the consumptive and non-consumptive effects of predators on prey and factors that influence patterns of predation is challenging because most prey have to contend with multiple predators with different functional traits. Each species of predator may respond to human activity differently and, hence, predator-specific approaches are necessary to fully understand predator-prey dynamics and how humans affect those dynamics. Therefore, identifying the explicit predator species within ecological communities and determining rates of predator-specific mortality can help elucidate the functional role specific predators play within ecological communities and how human land use influences predator-specific patterns of predation.

For the greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse), nest predation is the primary cause of nest failure and can influence population dynamics. A diverse suite of predators are known to predate sage-grouse nests and thus, generalizing about how specific habitat, landscape characteristics, and human land use influence nest fate has been challenging. Greater sage-grouse populations have declined across their range in western North America and declines have been attributed to habitat loss, habitat degradation, and land use. Many land use activities thought to be responsible for sage-grouse population declines are assumed to increase nest predation, yet few studies have evaluated the effects of

land use activities on explicit sage-grouse nest predators (e.g., the effects of land use on abundance and nest foraging behavior of specific predators). Domestic cattle (*Bos taurus*) grazing is often assumed to increase nest predation by reducing grass height (and hence nest concealment) and thereby facilitates nest detection by predators. Grass height is lower on actively grazed areas (hereafter pastures), but sage-grouse nest success appears to be similar on pastures grazed at varying intensities. The structural effects of livestock grazing (i.e., reduced nest concealment) could be offset by a numerical response of one or more sage-grouse nest predators to the presence of cattle (i.e., cattle may cause a localized numerical response in some nest predators). A reduction in the number of nest predators at the pasture scale could explain similar patterns of nest success on pastures grazed at varying intensities. That is, the effects of the two mechanisms (i.e., reduced nest concealment and a numerical response) could counteract each other if both were valid.

Chapter 1 evaluates one prediction of the numerical response hypothesis: a decreased probability of at least one sage-grouse nest predator predating sage-grouse nests in pastures with cattle relative to pastures without cattle present during the nesting season. Cameras placed at nest sites are often used to identify nest predators. However, deploying cameras can increase nest abandonment and affect nest fate by providing predators with olfactory and visual cues of nest locations. We leveraged the power of molecular methods to identify sage-grouse nest predators via predator DNA collected from eggshells from predated sage-grouse nests. We then used this information to evaluate the influence of habitat, nest-site characteristics, and grazing on predator-specific nest mortality. We also deployed artificial nests with trail cameras to determine the accuracy of our molecular method by comparing the predator species captured via trail camera with our molecular results. Our proof-of-concept study showed that non-invasive, molecular methods provide an accurate method for identifying nest predators. Our molecular analyses detected the species captured via trail camera at 95% of our artificial nests. We collected samples from 114 predated sage-grouse nests and detected predator DNA from 76 (67%) of those nests. We did not find evidence that domestic cattle grazing influenced predator-specific nest mortality. We found a negative relationship between shrub canopy cover and the probability of coyote (*Canis latrans*) predation and a negative relationship between ambient temperature and the probability of both coyote and corvid (*Corax spp.* and *Pica hudsonia*) predation. Our study highlights that

management efforts to increase sage-grouse nest success may vary spatially depending on the predominant predator within the system and that non-invasive genetic methods to determine predator-specific nest mortality can mitigate problems and biases associated with nest cameras.

Chapter 2 evaluates a second prediction of the numerical response hypothesis: one or more nest predator species avoid cattle by partitioning themselves in space and thus, are unavailable to consume sage-grouse nests on pastures with cattle. Additionally, the effects of grazing (i.e., reduced concealment at nests) could be offset if one or more nest predators partition themselves temporally to avoid cattle. Altering diel activity patterns could result in increased nest predator activity during portions of the day when they are less efficient at locating sage-grouse nests. We deployed motion-sensor cameras across six pastures to evaluate whether coyotes (a primary sage-grouse nest predator) altered spatiotemporal activity patterns in response to cattle. Contrary to the numerical response hypothesis, the probability of detecting coyotes was positively associated with cattle detections at camera sites. Moreover, coyotes did not shift their diel activity patterns in response to cattle being in the pastures. Thus, in our system, similar patterns of sage-grouse nest success in grazed and non-grazed pastures cannot be explained by the numerical response hypothesis or by a temporal avoidance of cattle by coyotes.

Our study did not find evidence to support the numerical response hypothesis. In our system, the presence of cattle did not influence predator-specific nest mortality. Further, the presence of cattle did not result in coyotes (the predominant nest predator in our system) altering their spatiotemporal activity patterns. In fact, we found that the probability of detecting coyotes increased with cattle detections suggesting that certain habitat characteristics (e.g., a relationship between increased forage quality for cattle and increased prey availability for coyotes) may offset any perceived risk that coyotes may have of cattle. Regardless, similar patterns of sage-grouse nest success on pastures with varying grazing intensity cannot be explained by the numerical response hypothesis. Current grazing practices (e.g., the number of cattle within a pasture and duration of grazing) may provide sage-grouse with areas of nesting refugia (i.e., areas within a pasture with adequate nest concealment) which could explain similar patterns of nest success on pastures grazed at

varying intensities. However, continued research evaluating explicit mechanisms that link domestic cattle grazing to sage-grouse demographics is needed.

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Dedication

To my son, Declan "Wolfie" Helmstetter, whose love, curiosity, and fascination about the natural world continues to inspire me as an ecologist and remind me why I chose this path. Never stop asking why.

Table of Contents

Abstract ii

Acknowledgments vi

Dedication vii

Table of Contents viii

List of Tables x

List of Figures xi

List of Equations xii

Statement of Contribution xiii

Chapter 1: Predator-Specific Mortality of Sage-grouse Nests Based on Predator DNA on Eggshells 1

INTRODUCTION 1

METHODS 5

Study Sites 5

Monitoring Sage-Grouse Nests 6

DNA Sample Collection from Predated Sage-Grouse Nests 6

Vegetation and Study Site Surveys 7

Proof-of-Concept Study 7

DNA Extraction and Species Identification 9

Molecular Analyses 11

Predator-Specific Nest Mortality Analysis 13

RESULTS 14

Molecular Analyses 14

Predator-Specific Mortality 17

DISCUSSION 17

Molecular Analyses – Artificial Nests 17
Molecular Analyses – Sage-Grouse Nests 20
Predator-Specific Mortality 22
LITERATURE CITED 25
Chapter 2: Where's the Beef? The Influence of Grazing on the Spatiotemporal Activity Patterns of a Primary Sage-Grouse Nest Predator 44
INTRODUCTION 44
METHODS 46
Study Sites 46
Data Collection 47
Coyote Space Use 47
Coyote Diel Activity Patterns 49
RESULTS 50
Coyote Space Use 50
Coyote Diel Activity Patterns 50
DISCUSSION 51
Coyote Space Use 51
Coyote Diel Activity Patterns 51
Sage-Grouse Management 52
LITERATURE CITED 54

List of Tables

Table 1.1. Variables considered in our suite of candidate models evaluating factors that influence predator-specific mortality 34
Table 1.2. Comparison of species-specific detections from trail cameras (column 1) and our molecular analysis (column 2 – 6) for the proof-of-concept study summarized across 35 nests that detected DNA 35
Table 1.3. Comparison of species-specific detections from trail cameras (column 1) and our molecular analysis (column 2 – 6) for the proof-of-concept study summarized across 86 samples that detected DNA 36
Table 1.4. Number of nest predator species detected (column 1) from predated sage-grouse nests and samples (columns 2 & 4) and the proportion of nests and samples each species was detected at (columns 3 & 5) 37
Table 1.5. Species detections by sample for the 18 sage-grouse nests that our molecular analysis detected >1 predator species. 38
Table 1.6. Top models (delta $AIC_c < 2$) evaluating detection of predator species via our molecular analysis by nest as a function of survey interval, temperature, precipitation, and total samples collected 39
Table 1.7. Top models (delta $AIC_c < 2$) evaluating detection of predator species via our molecular analysis by eggshell sample as a function of survey interval, temperature, and precipitation. 40
Table 1.8. Top models (delta $AIC_c < 2$) evaluating factors that influence predator-specific nest mortality of sage-grouse nests 41
Table 2.1. Model selection tables evaluating coyote occupancy at camera sites 60

List of Figures

Figure 1.1. The locations of our 5 study sites (black circles) in Idaho, USA. 42
Figure 1.2 Partial effects plots for response variables in the top models evaluating factors that influence predator specific mortality 43
Figure 2.1. The locations of our two study sites (black circles) 61
Figure 2.2. Probability of coyote detection at camera sites as a function of daily cattle detections 62
Figure 2.3. Non-parametric kernel density estimates of coyote diel activity patterns when cattle were present (dashed line) and when cattle were absent (solid line) 63
Figure 2.4. Non-parametric kernel density estimates of coyote diel activity patterns (dashed line) and cattle diel activity patterns (solid line) at trail camera sites where both species were detected 64

List of Equations

Equation 2.1. Occupancy models consist of two sub models..... 59

Statement of Contribution

NAH and CJC contributed to the study conceptualization, methodology, and formal analyses. NAH oversaw data collection and curation, wrote the first manuscript draft, and prepared data visualization for the manuscript. CJC acquired funding for the study and provided revisions of all manuscript drafts.

Chapter 1: Predator-Specific Mortality of Sage-grouse Nests Based on Predator DNA on Eggshells

INTRODUCTION

Predation is a ubiquitous ecological process that structures ecosystems and regulates prey populations via top-down effects across trophic levels (Estes et al. 2011, Ripple et al. 2014). Most species contend with a diverse suite of predators that vary in density, functional traits (i.e., foraging mode, morphology, and physiology), and habitat domain (Sih et al. 1998, Lima 2002, Schmitz 2017). Diversity in these traits among sympatric predators can cause variation in the consumptive and non-consumptive effects of the predator guild on prey populations (Miller et al. 2014, Schmitz 2017, Wirsing et al. 2021). In a sense, prey are trying to stay ahead of the proverbial predator-prey arms race (Dawkins and Krebs 1979, Abrams 1986) and multiple predators influence that coevolutionary relationship (Abrams 1991) whereby trait diversity among predators may stymie the prey's ability to adapt and reduce predation risk. Additionally, ecological gradients (e.g., vegetation structure) and disturbance (e.g., anthropogenic land use) can affect predator-prey interactions by influencing predator composition and abundance, encounter rates, availability of refugia, and spatiotemporal patterns of space use by both predator and prey (Kurki et al. 1998, Lyons et al. 2015, Hradsky et al. 2017). Thus, we need to identify the explicit suite of predators in each system and the proportion of predation events attributed to each predator so that predator-specific patterns of predation and the functional role specific predators occupy within ecological communities can be better quantified.

Identifying the predator responsible for discrete predation events (i.e., predator-specific mortality) is a critical step in elucidating the explicit mechanisms by which ecological gradients and disturbance influence predator-prey interactions. For example, road density was the best predictor of wolf (*Canis lupus*) and bear (*Ursus* sp.) predation on mountain caribou (*Rangifer tarandus caribou*) whereas forest successional stage better predicted cougar (*Puma concolor*) predation (Apps et al. 2013). Additionally, determining predator-specific mortality can also elucidate how the effects of predation on population dynamics can vary among predators. For example, ursid predation on neonatal elk (*Cervus canadensis*) was additive in multi-predator systems while predation of neonates by other

predators (e.g., canids and felids) was partially compensatory (Griffin et al. 2011). Thus, determining predator-specific morality and employing predator-specific analyses to better understand predator-prey relationships enhances our ability to make well-informed management decisions regarding prey populations and the relative importance of predation in prey population dynamics (Kunkel and Pletscher 1999, Griffin et al. 2011, Hradsky et al. 2017, Forrester and Wittmer 2019).

Nest predation is the primary cause of nest failure for many birds and, hence, can strongly influence habitat selection, life-history evolution, and population growth (Ricklefs 1969, Martin 1993, Taylor et al. 2012, Dillon and Conway 2018). Avian nest predator guilds are diverse, and can include many species of mammals, reptiles, and other birds (Newton 1998, Pietz and Granfors 2000, Coates et al. 2008, Kirkpatrick and Conway 2010). As a result, the effects of habitat attributes (e.g., vegetation structure and composition) on nest survival can vary across species, and also over ecological gradients in conjunction with predator composition and abundance (Benson et al. 2010, Coates and Delehanty 2010, Cox et al. 2012, Lyons et al. 2015). Determining predator-specific nest mortality is rare in avian nest predation studies despite the critical insights it can provide into causes of nest failure, and knowledge of a species' explicit nest predators can aid in local and regional efforts (e.g., habitat restoration or managing land use) to increase nest success and abundance of birds (Thompson 2007, Lahti 2009, Thompson and Ribic 2012).

Cameras placed at nest sites have been used for decades to document predator-specific nest mortality in birds (Larivière 1999, Richardson et al. 2009, Kirkpatrick and Conway 2010). However, deploying and maintaining cameras can disturb nest sites and increase the risk of nest abandonment and detection of nests by predators via visual and olfactory cues (Larivière 1999, Pietz and Granfors 2000, Williams and Wood 2002, Renfrew and Ribic 2003; but see Richardson et al. 2009). As a result, using cameras to document patterns of nest predation carries added risks of negatively affecting the ecological variable (i.e., nest fate) under study. Further, nest locations must be known prior to deploying cameras, and investigators risk missing predation events that occur prior to nest discovery or misallocating resources by deploying cameras at successful nests. Recent advancements in molecular techniques have provided powerful tools for assessing predator-specific mortality (Williams et al. 2003, Onorato et al. 2006). Predator DNA can be collected at kill sites from

saliva, hair, and scat, and used to infer the species of predator responsible for each mortality event (Onorato et al. 2006, Caniglia et al. 2013, Mumma et al. 2014). Yet, only a handful of studies have utilized these noninvasive techniques for determining the predator responsible for avian nest predation events (i.e., predator-specific nest predation; Steffens et al. 2012, Innes et al. 2015, Hopken et al. 2016). Building upon non-invasive methods for determining predator-specific nest predation (e.g., collecting predator DNA from predated nests) would therefore alleviate the negative effects of nest cameras while also providing valuable information regarding predator-specific patterns of nest predation.

Sage-grouse (*Centrocercus urophasianus* and *C. minimus*) populations have declined across their range (Coates et al. 2022) and declines have been attributed to land use, habitat loss, and habitat degradation (Beck and Mitchell 2000, LeBeau et al. 2014, Kirol et al. 2015, Sandford et al. 2017). Increased nest predation as a result of land use activities is one common mechanism proposed to explain sage-grouse population declines (Beck and Mitchell 2000, Knick and Connelly 2011, Webb et al. 2012). Nest predation is the primary cause of sage-grouse nest failure and population growth is sensitive to changes in nest success (Moynahan et al. 2007, Taylor et al. 2012). Thus, like many ground-nesting birds, changes in nest predator composition, predator abundance, or nest encounter rates could impact sage-grouse population dynamics (Evans 2004). Cameras have been used to identify common sage-grouse nest predators and the habitat characteristics associated with nest success can vary in relation to predator species (Coates and Delehanty 2010). However, a significant knowledge gap still exists regarding how heterogeneity in habitat and land use influence predator-specific probabilities of sage-grouse nest predation despite nest fate playing a key role in juvenile recruitment and sage-grouse population dynamics (Moynahan et al. 2007, Coates and Delehanty 2010, Taylor et al. 2012, Coates et al. 2016).

Domestic cattle (*Bos taurus*) grazing (hereafter grazing) is the primary land use activity across much of the sagebrush biome in western North America (Veblen et al. 2014). Grazing is often assumed to adversely affect sage-grouse recruitment by reducing residual grass height (and hence nest concealment), thereby increasing nest predation risk by facilitating olfactory and visual detection of nests by predators (Beck and Mitchell 2000). The nest concealment hypothesis is commonly proposed to explain variation in nest fate in birds (Borgmann and Conway 2015). For sage-grouse, the nest concealment hypothesis

hinges on evidence that grass height influences sage-grouse nest success (Doherty et al. 2014) and predicts that both grass height at sage-grouse nests and average nest success will be lower in actively grazed areas (hereafter pastures) compared to non-grazed pastures. While grass height at both random points and nest sites is indeed lower on pastures grazed at higher intensities (i.e., pastures with more cattle per acre and/or increased grazing durations), recent evidence found little support for the hypothesized effects of grazing on nest fate at the pasture scale (Smith et al. 2018). No differences in sage-grouse nest success among pastures grazed at different intensities suggests that either grazing fails to induce the increased nest detection by predators as commonly predicted by the nest concealment hypothesis, or grazing does induce increased nest detection, but that increase is offset by localized numerical responses of one or more nest predators (i.e., reduced predator density within pastures while cattle are present). Hence, identifying predator-specific causes of nest failure is critical to understanding causal mechanisms linking grazing to patterns of sage-grouse nest success, so that land managers can balance grazing activities with sage-grouse conservation.

A negative numerical response of predators due to increased human and human-associated activity (i.e., the presence of cattle and ranchers) could explain why sage-grouse nest success does not differ among pastures grazed at different intensities despite the reduction in grass height on more heavily grazed pastures (Smith et al. 2018). Mammalian carnivores will often partition themselves in space and/or time to avoid human activity (Van Dyke et al. 1986, Moll et al. 2018, Suraci et al. 2019). While several mechanisms can drive these shifts in predator foraging activity (e.g., fear, persecution, hunting, or changes in prey abundance), a local reduction in the number of predators could reduce the consumptive and non-consumptive effects of predation on prey populations. The numerical response hypothesis predicts a decreased probability of at least one sage-grouse nest predator predating sage-grouse nests in pastures with livestock relative to pastures without livestock present during the nesting season. Under the numerical response hypothesis, increased nest detection due to reduced cover could still occur (i.e., the numerical response hypothesis is not an alternative to, or mutually exclusive of, the nest concealment hypothesis). However, a negative numerical response by one or more sage-grouse nest predator(s) to human activity could dampen the effects of increased nest detection by reducing the number of predators

within pastures with active grazing. That is, the effects of the two mechanisms would counteract each other if both were valid.

Our objectives were: 1) evaluate the efficacy of using a non-invasive molecular technique to identify sage-grouse nest predators, and 2) test whether the numerical response hypothesis counteracts the reduced concealment in grazed pastures by testing explicit predictions regarding how livestock grazing, habitat, and nest-site characteristics influence predator-specific nest predation. We tested the following prediction of the numerical response hypothesis: the probability of mammalian nest predation on sage-grouse nests will be lower on pastures with concurrent livestock grazing. Additionally, we tested whether 1) increased nest concealment (e.g., sagebrush canopy cover and visual concealment at nest sites) reduced the probability of avian nest predation, 2) landscape features associated with mammalian predator movement (e.g., undeveloped roads and fence lines) and space use (e.g., water sources) increased the probability of mammalian nest predation, and 3) landscape characteristics that facilitate nesting and perching of avian nest predators or offer potential subsidies (e.g., trees or land converted to agriculture) increased the probability of avian nest predation.

METHODS

Study Sites

We conducted research across 5 study sites in Owyhee, Twin Falls, Cassia, Butte, and Custer counties, Idaho (Fig. 1.1; Conway et al. 2019). Elevation at the study sites ranged from 1400 – 1900-m. Common overstory species included Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), little sagebrush (*Artemisia arbuscula*), three-tip sagebrush (*Artemisia tripartita*), rubber rabbitbrush (*Ericameria nauseosa*), and green rabbitbrush (*Chrysothamnus viscidiflorus*) (Conway et al. 2019). Sandberg bluegrass (*Poa secunda*), bottlebrush squirreltail (*Elymus elymoides*), bluebunch wheatgrass (*Pseudoroegneria spicata*), western wheatgrass (*Pascopyrum smithii*), and needle grass (*Acnatherum spp* and *Hesperostipa spp*) were common understory species (Conway et al. 2019). The study sites were remote with little development in the surrounding area and were actively used as nesting habitat by sage-grouse hens (Conway et al. 2019). Common sage-grouse predators at our study sites included coyote (*Canis latrans*), American badger

(*Taxidea taxus*), red fox (*Vulpes vulpes*), bobcat (*Lynx rufus*), raven (*Corvus corax*), crow (*Corvus brachyrhynchos*), and magpie (*Pica hudsonia*). The study sites consisted of a patch work of fenced pastures designed to keep domestic cattle in (or out) while remaining permeable to wildlife. The land at the study sites was managed by the U.S. Bureau of Land Management (BLM) and was leased by the BLM to permittees who use their cattle to graze the pastures. Grazing management guidelines that restrict the intensity, timing, and frequency of grazing were in place at our study sites.

Monitoring Sage-Grouse Nests

We used spotlights and hand nets to capture sage-grouse hens at night (Wakkinen et al. 1992, Conway et al. 2019) in February and March of 2020 and 2021. We fitted sage-grouse hens with a necklace type VHF radio-transmitter (Advanced Telemetry Systems, Isanti, MN) and attempted to monitor radio-marked hens every 2 – 3 days. We assumed a hen was nesting when we consistently located the hen in the same area for 2 – 3 monitoring occasions. We minimized the number of times we were within 100-m of a nest and tried to never flush a hen off her nest. We triangulated each hen's location and identified the potential shrub or cluster of shrubs that the hen was likely nesting under. We used binoculars to locate and confirm nests visually when possible. We established monitoring points 90˚ to 150˚ apart and took bearings to nesting hen locations. We considered hens to be incubating a nest if the bearings were consistent for 2-3 monitoring occasions. We carried out visual inspections of nests when hens were away from their nests during a monitoring occasion to determine whether nests had been predated. We fitted a subset of hens at one study site with Platform Transmitting Terminal (PTT) backpacks and we monitored those hens via GPS locations downloaded remotely. We located nests in-person and determined nest fate when the GPS locations of a hen were inconsistent with nesting behavior and movement.

DNA Sample Collection from Predated Sage-Grouse Nests

We collected predator DNA from eggshells at predated nests by either swabbing eggs and eggshell fragments or collecting eggshell fragments. We wore gloves to avoid contaminating samples. We dipped swabs (foam swab with polystyrene handle, 25-1506 1PF 100, Puritan Medical Products) into phosphate buffered saline (PBS; pH 7.0, 1.37M NaCl, 27mM KCl, 100mM Na_2HPO_4, 18mM KH_2PO_4) prior to swabbing the eggshells. We

swabbed the entire surface area (exterior and interior) of any eggshell fragment larger than 1/8 of an entire egg. If eggs were nearly whole (e.g., if an avian nest predator pecked a hole in the egg to remove the contents without breaking the egg apart) we only swabbed the exterior of the egg and concentrated swabbing around the edges of the hole. We used one swab per egg. When we could only locate eggshell fragments, we estimated how many fragments made up an entire egg and used one swab per the group of fragments we estimated as one egg. We broke the handle off the swabs and stored swabs in 2-mL screw top tubes with 0.7-mL of Queens Lysis Buffer (0.1M Tris (pH 8.0), 0.1M EDTA (pH 8.0), 0.01M NaCl, 0.5% SDS). We collected any eggshell fragments that were <1/8 of an entire egg and stored them in 15-mL tubes (Nalgene Straight-Side Jar) with 2-mL of Queens Lysis Buffer, ensuring that all eggshell fragments were submerged in the buffer. We collected field negatives at four of the study sites by swabbing and collecting eggshell fragments from successful sage-grouse nests (n = 10 nests, 54 samples) using the methods described above.

Vegetation and Study Site Surveys

We conducted vegetation surveys at successful and failed sage-grouse nests following procedures outlined in Conway et al. (2019). Briefly, vegetation surveys included several components: 1) photographs taken of a 20-cm pink ball placed in the nest bowl to estimate nest concealment from 4 sides (lateral concealment) and top down (aerial concealment), 2) two 30-m line-intercept transects to estimate percent shrub canopy cover, average grass height, average of grass removed (i.e., grazing intensity), and average effective cover of vegetation, 3) estimates of percent vegetation cover from Daubenmire plots, and 4) a count of new and old wildlife and domestic livestock fecal droppings along the 30-m line-intercept transects (Conway et al. 2019). Additionally, we surveyed study sites and recorded locations of perches that could be utilized by avian predators as well as ephemeral and perennial water sources.

Proof-of-Concept Study

We deployed artificial nests with motion-sensor trail cameras (Cuddeback 8mp and 20mp White Series and Reconyx Hyperfire models) to compare the accuracy of our molecular results to the predator species captured via trail cameras. We deployed artificial nests at four of our study sites (Fig. 1.1). We placed 4 – 5 white or brown domestic chicken

(*Gallus gallus domesticus*) eggs within sagebrush shrubs to loosely mimic greater sage-grouse nests. Our goal was to collect DNA samples from predated nests and, thus, our artificial nests and cameras were relatively conspicuous except for when we targeted mammalian predators. We deployed olfactory lures at each nest consisting of either commercially available predator lure (e.g., Dunlap's Predator Bait) and/or carnivore urine (*Vulpes* sp. or coyote urine) placed on an absorbent cloth and hung from the shrub branches). Additionally, we placed visual lures (e.g., feathers hung from the shrub branches) at some artificial nests. We monitored artificial nests every 1 – 2 days. We secured trail cameras to t-posts and aimed the camera at the "entrance" of the artificial nests (i.e., a small gap in shrub cover that a sage-grouse could enter and exit through). We set trail cameras to take a burst of 5 photos continuously (i.e., no delay between bursts) when the sensor was triggered by motion. Once we discovered that an artificial nest was predated, we immediately collected DNA from eggshells using the methods described above. Additionally, we used two alternative storage methods when enough eggshell remains were available: 1) we stored swab(s) in a 15-mL tube with a desiccant capsule (Dri-Capsules, SGC-50, Isohelix) separated from the swab by a chemical wipe, and 2) we stored eggshell fragments in a 50-mL tube with 5-mL of desiccant beads (Silica Gel, S161-212, Fisher Chemical) separated from the eggshells by a chemical wipe. We used logistic regression with a logit link and binomial distribution to evaluate whether detection (i.e., a binary response variable representing non-detections and detections via our molecular analysis) was influenced by storage method. We evaluated the influence of storage method on detection by sample (and not by nest) because multiple storage methods were used per artificial nest. Cost for materials per sample varied among storage methods: $0.47 for eggshells stored in 50-mL tubes with desiccant beads, $0.82 for swabs stored in 2-mL tubes with 0.7-mL of buffer, $2.56 for eggshells stored in 15-mL tubes with 2-mL of Queens Lysis Buffer, and $4.54 for swabs stored in 15-mL tubes with a desiccant capsule. However, cost per sample does not include lab time or lab materials (i.e., DNA extraction; described below) which can vary based on the amount of Queens Lysis Buffer used in the storage and extraction process. We redeployed new eggs when nests were predated (or left non-predated eggs in the nest) and considered it a new nest in our analysis (described below).

DNA Extraction and Species Identification

We extracted, amplified, and analyzed all DNA samples collected from both artificial and real sage-grouse nests at the Laboratory for Ecological, Evolutionary, and Conservation Genetics at the University of Idaho in a laboratory dedicated to processing low quality DNA samples. DNA was extracted from samples using the Qiagen DNeasy Blood and Tissue Kit with the following protocol modifications. We combined 600-µL of the Queens Lysis Buffer from the tube that contained the 40-µL of proteinase K in 2-mL tubes. We added the swabs that were stored with desiccant beads to a tube with 600-µL of Queens Lysis Buffer and 40-µL of proteinase K. We pipetted up to 2-mL (but less if possible) of Queens Lysis Buffer over the eggshell fragments stored in tubes with desiccant beads to "wash" any DNA off the fragments into the tube. We then combined the Queens Lysis Buffer that washed over the eggshell fragments with 40-µL of proteinase K in 2-mL tubes. We used multiple 2-mL tubes if >600-µL was used for the storage method (e.g., the eggshell fragments stored in 2-mL of Queens Lysis Buffer). We removed the foam tip from the handle of the swabs and left the foam tip in the 2-mL tubes with the Queens Lysis Buffer and proteinase K. We vortexed each 2-mL tube with Queens Lysis Buffer and proteinase K for 10 seconds and incubated the tubes overnight at 56°C. After incubation, we added 600-µL of buffer AL (Qiagen) to the solution, vortexed the samples for 10 seconds, and incubated the samples at 70°C for 10 minutes. We then added 600-µL of 100% ethanol to the solution, vortexed the tubes for 10 seconds, and transferred 600-µL of the solution from each tube into a spin column with a filter that was then placed into a collection tube. We used a single spin column for all the 2-mL tubes associated with an individual sample. We centrifuged spin columns at 10,000 rpm for 1 minute and discarded the solution that passed through the filter. We repeated the process until all the solution from a sample had been filtered. We added buffer AW1 (Qiagen) to the spin columns and centrifuged the tube at 10,000 rpm for 1 minute and discarded the solution that passed through the filter. We then added buffer AW2 (Qiagen) to the spin columns and centrifuged the tube at 12,000 rmp for 1 minute and discarded the solution that passed through the filter. We placed the spin column into a 1.5 mL microcentrifuge tube, added 200-µL of buffer AE (Qiagen), and centrifuged the spin column at 10,000 rpm for 1 minute. Lastly, we pipetted the contents collected in the microcentrifuge

tube back into the spin column and centrifuged the spin column again at 12,000 rmp for 1 minute. Negative controls were used in each extraction.

We conducted two independent species ID multiplex PCRs and separate fragment analyses on every sample: 1) a newly developed corvid mtDNA fragment analysis designed to distinguish magpies from ravens/crows (i.e., we could not distinguish between ravens and crows; *Corvus corax and C. brachyrhynchos*), and 2) a mammalian fragment analysis that can identify 16 wild mammalian carnivores including potential sage-grouse nest predators at our study sites (coyote, bobcat, and red fox; Davidson et al. 2014, De Barba et al. 2014). Both methods consist of the co-amplification and fragment analysis of segments of the mtDNA control region (canid, ursid, and mustelid) or the cytochrome b region (felid and corvid) using dye-labeled primers. The corvid analysis used one dye-labeled forward primer Corvid F 5-'TTCTCAGCAATCCCATACATT-3' and two reverse primers CcoraxBrach R 5-'GGGCGTGAAATTTTCTGGG-3'and Phudsonia R 5-'TGCTATAGTAGCAAGTAGGG-3'. The mammalian predator analysis used two dye-labeled forward primers SIDL 5-'TCTATTTAAACTATTCCCTGG-3' (Murphy et al. 2000) and FelidID F 5'-TACATACATGCYAACGGAGC-3' (Davidson et al. 2014) and four different reverse primers: H16145 5'-GGGCACGCCATTAATCGACG-3' (Murphy et al. 2000, De Barba et al. 2014), H3R 5'-CCTGAAGTAGGAACCAGATG-3' (Dalén et al. 2004), LRuf R 5'-CCGAATATTTCATGTCTCTGAA-3' (Davidson et al. 2014), and PCon R 5'-ATGACCGCAAATAGTAGTATGA-3' (Davidson et al. 2014). We used the polymerase chain reaction (PCR) to amplify DNA fragments. The PCR for the mammalian fragment analysis contained 1X QIAGEN Multiplex PCR Master Mix, 0.7X Qiagen Q Solution (Qiagen Inc.), 0.29-µM SIDL, 0.20-µM H16145, 0.13-µM FelidID F, 0.10-µM H3R, 0.03-µM LRuf R, 0.03-µM PCon R, and 1-µL of DNA extract in a 7-mL reaction volume. The thermal profile for the mammalian fragment analysis was an initial denaturation step of 95°C for 15 minutes followed by 35 cycles of 94°C for 30 seconds, 46°C for 1.5 minutes, 72°C for 1 minute, 60°C for 30 minutes, and 4°C for 10 minutes. The PCR for the corvid fragment analysis contained 1X QIAGEN Multiplex PCR Master Mix, 0.7X Qiagen Q Solution (Qiagen Inc.), 0.07-µM Corvid F, 0.10-µM CcoraxBrach R, 0.10-µM Phudsonia R, and 1-µL of DNA Extract. The thermal profile for the corvid fragment analysis was an initial denaturation step of 94°C for 15 minutes followed by 13 cycles of 94°C for 30 seconds, a

touchdown at 65°C for 90 seconds with a reduction in temperature by 0.4°C each cycle, and 72°C for 1 minute followed by 37 cycles of 94°C for 30 seconds, 60°C for 90 seconds, and 72°C for 1 minute and lastly 60°C for 30 minutes and 4°C for 10 minutes. We loaded PCR products onto an ABI3130xl DNA sequencer and used Genemapper software (Applied Biosystems) to score fragments using size-specific bins for species. We used both positive and negative controls in each PCR, and all samples were run in duplicate.

We also collected DNA samples (tissue, blood, and feathers) from American badgers, magpies, ravens, crows, and raccoons (*Procyon lotor*) within our study region. Samples were collected from roadkill, private trappers, and incidental carcasses that we located. Samples were stored in 1.4-mL of DETS buffer (tissue), with desiccant beads (tissue from private trappers), and on Nobuto strips (blood), and extracted using a Qiagen DNeasy Blood and Tissue Kit. We used these samples as well as pre-extracted samples of coyote, red fox, grey fox (*Urocyon cinereoargeteus*), wolf (*Canis lupus*), dog (*Canis lupus familiaris*), sage-grouse, and weasel species (*Mustela spp*.) as positive controls in our molecular analyses and to test for co-amplification between species (e.g., corvid primers amplifying coyote DNA). Lastly, we evaluated whether the primers in the mammalian fragment analysis would amplify a unique American badger DNA fragment length that would allow us to detect American badger DNA from predated sage-grouse nests.

Molecular Analyses

We calculated detection and accuracy metrics by nest (i.e., combining all samples collected at a nest) and by sample (i.e., individual swab or tube with eggshell fragments) for our proof-of-concept study. We calculated detection by nest by dividing the number of artificial nests in which at least one sample detected DNA by the total number of artificial nests for which we collected samples. We calculated detection by sample by dividing the number of samples collected from artificial nests that detected DNA by the total number of samples collected. We calculated accuracy of detecting nest predators of artificial nests via our molecular analysis (and samples collected from artificial nests) by dividing the number of artificial nests (or samples collected from artificial nests) that detected the species captured via trail camera by the number of nests (or samples collected from artificial nests) that detected nest predator DNA. We used two approaches when evaluating accuracy for

artificial nests: 1) a less-conservative approach where we considered nests and samples accurate if our molecular analysis detected the species captured via trail camera irrespective of whether they detected an additional species not captured via trail camera, and 2) a more-conservative approach where we considered nests and samples inaccurate if our molecular analysis detected the species captured via trail camera as well as a different species not captured via trail camera. We calculated detection for cameras deployed at artificial nests by dividing the number of cameras that captured predation events by the total number of cameras deployed. We also calculated detection for real sage-grouse nests by nest and by sample by dividing the number of nests (or samples) that detected DNA by the total number of nests that samples were collected from (or the total number of samples collected). DNA degradation is influenced by the amount of time DNA is in the environment, UV radiation, and moisture. We used logistic regression with a logit link and binomial distribution to evaluate whether detection was influenced by the final survey interval length (i.e., the amount of time between when a sage-grouse nest was surveyed and considered active and when the nest was discovered predated), the number of samples collected at a nest, sum of precipitation during the final survey interval (PRISM Climate Group), average minimum, maximum, and mean temperature during the final survey interval (PRISM Climate Group), and an interaction term between average temperature during the final survey interval and precipitation. We evaluated the influence of these variables on detection by nest and by sample (but did not include the number of samples per nest as a covariate in the by-sample analysis). We standardized all variables by subtracting the mean and dividing by the standard deviation. When 2 predictor variables were correlated (i.e., Pearson correlation coefficient of >0.70), we ran univariate multinomial logistic regression models for each correlated variable and selected the variable to include in our model based on Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). After removing correlated variables, we compared all subsets of our global model using the *MuMIn* package (Bartoń 2022) in R (R Core Team 2023) and selected our top model based on AIC_c.

We quantified the proportion of specific nest predator species detected at sage-grouse nests by dividing the total number of species-specific detections across all sampled sage-grouse nests by the total number of sage-grouse nests that detected any nest predator DNA. We also quantified the proportion of individual nest predators detected per DNA sample by

dividing the total number of samples that detected a specific nest predator species by the total number of samples that detected nest predator DNA. When an individual nest detected multiple species via one or more samples collected from that nest, we assigned a proportion of that detection to each of the species detected. For example, if samples collected from an individual nest detected both raven/crow and coyote DNA, we assigned 0.5 to the proportion of nests that detected raven/crow and 0.5 to the proportion of nests that detected coyote. Similarly, if a single sample detected multiple species, we assigned a proportion of that detection to each species detected. For example, if a single sample detected both raven/crow and coyote DNA, we assigned 0.5 to the proportion of samples that detected raven/crow and 0.5 to the proportion of samples that detected coyote. Multiple predator DNA on an egg can reflect a scenario where a second predator scavenges remains of nest contents that were initially predated by a different predator species (but we have no way of distinguishing which predator was the initial and which was the scavenger).

Predator-Specific Nest Mortality Analysis

We used multinomial logistic regression to evaluate how land use, nest-site characteristics, and habitat influenced nest fate accounting for predator species. For this analysis, we excluded nests that did not have grazing and/or vegetation data associated with them. We pooled raven/crow and magpie detections due to low sample sizes of corvid detections at sage-grouse nests. Further, we only included nests where coyote was the only mammalian species detected via our molecular analysis due to a small sample size of other mammalian nest predator detections (i.e., American badgers; n = 2 nests). Thus, our response variables were successful nests (i.e., nests that hatched 1 or more egg; n = 102 nests), failed nests in which only coyote was detected via our molecular analysis (n = 37 nests), and failed nests in which only a corvid species (i.e., magpie, raven/crow, or both) was detected via our molecular analysis (n = 12 nests). We considered 23 variables believed *a priori* to be related to predator-specific patterns of nest predation (Table 1.1). We standardized all variables by subtracting the mean and dividing by the standard deviation. When 2 predictor variables were correlated (i.e., Pearson correlation coefficient of >0.70), we ran univariate multinomial logistic regression models for each correlated variable and selected the variable to include in our global model based on AIC_c. The biological effects of environmental variables can be influenced by the scales of observation for covariate data (McGarigal et al. 2016; Wiens,

1989). We considered several spatial scales of shrub canopy cover (8-km and 44-km; Table 1.1) based on the estimated home range and breeding range size of ravens (6.6-km and 40.5-km, respectfully; Smith and Murphy 1973, Bruggers 1988) and the home range size for coyotes (37 – 47-km; Hernendez and Laundre 2003). We also considered shrub canopy cover at nest sites estimated from the two 30-m line transects and intermittent scales between the estimated raven breeding range and coyote home range sizes (i.e., 14-km and 22-km; Table 1.1). To optimize the spatial scale of shrub canopy cover, we ran univariate multinomial logistic regression models for each scale and selected the optimal scale based on AIC_c. We reduced our candidate set of predictor variables further by running univariate multinomial logistic regression models for variables that would influence the probability of predation by a specific predator species in similar ways (e.g., distance to powerlines, perch sites, and nest sites) and selected the variable to include in our model based on AIC_c. We used the *MuMIN* package (Bartoń 2022) in R (R Core Team 2023) to compare all subsets of our global model and selected our top model based on AIC_c. We explored partial effects plots for each of the variables included in the top models (i.e., delta AIC_c <2) that had 95% confidence intervals (CIs) that did not overlap 0.

RESULTS

Molecular Analyses

We collected a total of 133 samples from 42 artificial nests (range = 1 – 8 samples per artificial nest). Using American badger positives, we determined that the existing primers in the mammalian fragment analysis amplified a unique fragment length of 320.98 – 326.74 base pairs that could be used to identify American badger. We detected raven/crow, magpie, coyote, American badger, and bobcat via our molecular analysis and raven, magpie, and coyote via our trail cameras on 37 artificial nests (Table 1.2 & 1.3). We had four predated artificial nests where the camera malfunctioned (i.e., did not take any photos of the predation event) and thus, detection for cameras deployed at artificial nests was 90%. We also collected two samples (one swab sample and one eggshell fragment sample) from a stray chicken egg found by a fence (likely moved by a predator from a nearby artificial nest). The four nests where the camera malfunctioned detected magpie for nine of the ten samples collected and the two samples collected from the stray egg detected raven/crow. The four artificial nests

where the camera malfunctioned and the stray egg were included in our detection analysis but excluded from our accuracy analysis. Our detection by nest and by sample was 95% and 73%, respectively. Our molecular analyses detected a species not captured via trail camera at 8 artificial nests (Table 1.2), but the molecular analysis also detected the species captured via trail camera at 6 of those 8 artificial nests (Table 1.2). A total of 13 samples collected from the 8 artificial nests (1 – 4 samples per nest) detected a species not captured via trail camera, but our molecular analysis also detected the species captured via trail camera for 6 of the 13 samples (Table 1.3). Thus, our accuracy by nest and by sample when using our less-conservative approach (i.e., considering nests and samples accurate when they successfully detected the species captured via trail camera regardless of whether they also detected a second species) was 94% and 93%, respectively. Conversely, our accuracy by nest and by sample when using our more-conservative approach (i.e., considering nests and samples as inaccurate when they detected the species captured via trail camera as well as a different predator species) was 74% and 80%, respectively. Detection was 68% for swabs stored with desiccant capsules, 76% for swabs stored with Queens Lysis Buffer, 69% for eggshell fragments stored with Queens Lysis Buffer, and 83% for eggshell fragments stored with desiccant beads. Results from our logistic regression indicated that storage method did not influence probability of detection (i.e., 95% CIs for all storage methods overlapped 0).

We collected 651 samples at 124 sage-grouse nests: 594 samples from 114 predated sage-grouse nests and 57 samples from 10 successful sage-grouse nests that were used as field negatives. We detected raven/crow, magpie, coyote, red fox, American badger, and cougar via our molecular analysis from the 594 samples collected from predated sage-grouse nests (Table 1.4). Predators were detected at 76 (67%) of the 114 predated sage-grouse nests (excluding hatched nests). Predators were detected from 201 (34%) of the 594 samples collected from predated sage-grouse nests. We detected magpie via our molecular analysis from a single sample collected from one hatched nest (i.e., from 1 of the 57 field negative samples) and detected no predator DNA from the other 56 field negative samples. We detected multiple predator species from samples collected from 18 predated sage-grouse nests (Table 1.5). We collected 1 – 10 samples ($\mu = 6.90$) per sage-grouse nest from the 18 nests that our molecular analysis detected multiple nest predator species, and 1 – 11 samples ($\mu = 4$) per sage-grouse nest from the 58 nests that our molecular analysis detected only a

single nest predator species. At the 58 nests where we detected a single nest predator, we detected predator DNA on 43% (n = 130) of the 303 samples collected (the remaining 57% of samples yielded no predator DNA) and 91% (n = 53) of the 58 nests with >1 sample collected had that single predator's DNA. We detected predator DNA from only 1 sample at 45% (n = 26) of the 58 nests (including nests where only 1 sample was collected). At the 18 nests where we detected >1 nest predator, we detected nest predator DNA from 57% (n = 71) of the 124 samples (the remaining 43% of samples yielded no predator DNA). Lastly, 56% of the 18 nests where we detected >1 predator had >1 sample that detected DNA for both nest predators (Table 1.5).

Due to stochastic co-amplification of sage-grouse DNA by our raven/crow primers (i.e., the Corvid F and CcoraxBrach primers), we increased the annealing temperatures of our corvid fragment analysis to 61.8°C until the raven/crow primers no longer amplified sage-grouse DNA. We re-ran any samples collected from predated sage-grouse nests that detected raven/crow with only the raven/crow primers at the increased annealing temperature described above. Additionally, we found that magpie positives (i.e., tissue samples) simultaneously amplified both the fragment length associated with magpie (279.55 – 280.75 base pairs) and the fragment length associated with raven/crow (324.7 – 326.61 base pairs). Thus, using only the raven/crow primer (as described above) allowed us to determine whether our molecular analysis was detecting only magpie DNA or both magpie and raven/crow DNA from sage-grouse and artificial nests. Interestingly, 214 samples collected from sage-grouse nests amplified one of two fragment lengths associated with wolf/domestic dog (365 – 368; De Barba et al. 2014) in the mammalian fragment analysis. We determined that the primers used in the mammalian fragment analysis were co-amplifying sage-grouse DNA by including sage-grouse positives in our analyses. Thus, we were unable to distinguish whether we were detecting sage-grouse or wolf/domestic dog from DNA collected from predated sage-grouse nests. Lastly, on 32 occasions we were unable to collect samples from predated sage-grouse nests because no eggshell remains were found at or around the sage-grouse nest site.

Final survey intervals for sage-grouse nests ranged from 1 – 10 days with an average of 3.12 days. We collected 1 – 11 samples per nest from predated sage-grouse nests with an

average of 5.43 samples/nest. We found no evidence that survey interval, number of samples per nest, ambient temperature, or precipitation affected detection of DNA on eggshells of predated nests; the top detection model was the null model regardless of whether we evaluated detection by nest (Table 1.6) or by sample (Table 1.7) and the covariates included in all models with a ΔAIC_c of <2 had 95% CIs that overlapped 0.

Predator-Specific Mortality

We used 15 predictor variables in the global model after removing correlated candidate variables and optimizing the scale for shrub canopy cover (bolded variables in Table 1.1). Shrub canopy cover influenced the probability of nest predation by coyotes, distance to a perennial water source influenced the probability of nest predation by corvids, and minimum temperature influenced the probability of nest predation by both corvids and coyotes. All other predictor variables included in the top models (Table 1.8) had CIs that overlapped 0. Shrub canopy cover was negatively associated with the probability that a coyote predated a nest (top model beta = -0.67, top model 95% CIs = -1.19 – -0.14), distance to a perennial water source was positively associated with the probability a corvid predated a nest (top model top model beta = 0.91, top model 95% CIs = 0.28 – 1.54), and average minimum temperature during the final survey interval prior to nest predation was negatively associated with the probability that either a coyote (top model beta = -0.46, top model 95% CIs = -0.91 – -0.01) or a corvid (top model beta = -1.03, top model 95% CIs = -1.79 – -0.27) predated a nest (Fig. 1.2). Model weight was relatively low for all top models (9.1%; Table 1.8). Therefore, we visually compared shrub canopy cover, distance to a perennial water source, and average minimum temperature partial effect plots to the partial effects plots of the same variables from model-averaged estimates that encompassed 95% of the model weight to ensure that the relationships between the predictor and the probability of coyote or corvid nest predation were consistent across all models and they were (Fig. 1.2).

DISCUSSION

Molecular Analyses – Artificial Nests

Identifying the explicit predator responsible for a predation event is a critical step in quantifying predator-prey relationships (Griffin et al. 2011, Mumma et al. 2014, Hradsky et

al. 2017, Forrester and Wittmer 2019). Our proof-of-concept study highlights that molecular techniques are an accurate method to identify both avian and mammalian nest predators from eggshell fragments at predated nests. Detection of predator DNA from artificial nests was higher when evaluated by nest (i.e., pooling samples per artificial nest) than when evaluated by sample (i.e., by egg or eggshell fragments). Thus, like other studies, our proof-of-concept results suggest collecting multiple samples from prey remains (in our case 1 swab per egg for multiple eggs per nest) is an important component of increasing success rates for identifying predators via molecular techniques (Sundqvist et al. 2008, Mumma et al. 2014). Accuracy for detecting the true nest predator on artificial nests was 94% (by nest) and 93% (by sample) when evaluated using our less-conservative approach (i.e., considering nests and samples accurate if they detected the species captured via trail camera irrespective of whether they detected an additional species not captured via trail camera) and 74% (by nest) and 80% (by sample) when evaluated using our more-conservative approach (i.e., considering nests and samples that detected >1 predator species as inaccurate if the trail camera only detected 1 of them). Previous studies that utilized nest-cameras to evaluate the efficacy of molecular techniques for nest predator identification reported accuracies of 44.4 and 50% (Steffens et al. 2012 and Hopken et al. 2016, respectively). Thus, regardless of which method we used to evaluate accuracy, our proof-of-concept results indicate identifying nest predators via molecular techniques is more accurate than previously reported. From an applied perspective, we consider our more-conservative approach a better representation of the efficacy of our molecular method if quantifying predator-specific patterns of nest predation is the management objective. That is, multiple predator species may be detected via our molecular method due to scavenging events and the inability to distinguish between the initial nest-predator and scavenger should be accounted for when considering the use of our molecular method in evaluating predator-specific nest mortality. Lastly, when grouping avian and mammalian species into functional groups (i.e., corvids and mammals), our more-conservative estimate of accuracy is even higher: 80% by nest and 87% by sample. Factors that influence predator-specific patterns of nest predation (e.g., ecological gradients or land use) among functional groups are likely similar and thus, pooling results by functional group is informative for avian conservation and management efforts.

On 4 occasions trail cameras did not capture a species predating our artificial nests despite the cameras remaining functional the whole time. Thus, detection of nest predators via cameras was not 100% (in our case camera detection was 90%). Further, eggs were often moved from the viewshed of the camera and therefore, we were unable to determine from the camera data if an additional species scavenged the eggs after the initial predation event. We suspect that subsequent scavenging may explain why 12 samples from 8 artificial nests detected DNA from species that were not captured via trail cameras. Our results indicate that camera results are not perfect (despite that assumption in our calculations of 'accuracy' for our molecular methods) and both molecular methods and the use of cameras for identifying nest predators can suffer from detection and/or accuracy issues (Coates and Delehanty 2010, Hopken et al. 2016, Taylor et al. 2017). Thus, taking steps to increase camera detections (e.g., using higher-quality batteries, using continuously recording cameras, or using >1 camera per nest) and increasing the area that animals can be detected (e.g., include additional cameras that monitor larger viewsheds) would be helpful in future proof-of-concept studies.

Field collection and preservation (i.e., storage) methods of low-quality DNA (e.g., nest predator saliva collected from predated eggshells) can influence DNA amplification success rates (Murphy et al. 2000, Roon et al. 2003, Wultsch et al. 2015). Additionally, storage methods can vary in cost and balancing the allocation of resources (i.e., time and money) is often a necessity in wildlife conservation and management. Detection ranged from 68 – 83% across our 4 storage methods, but we found no evidence that storage method affected the probability of detecting DNA. Thus, storage methods that reduce overall cost and laboratory time may be applicable for identifying avian nest predators via our molecular method. Based on cost per sample, while accounting for lab time and materials, the swabs stored in buffer were the cheapest method. While eggshells stored in silica appear cheaper, increased lab time and materials resulted in this storage method being more costly. However, our sample sizes varied from 19 – 49 per storage method and we did not account for factors that influence DNA degradation prior to sample collection (e.g., whether there was variation in exposure to UV radiation among samples collected from individual nests). Therefore, we suggest a more in-depth analysis of storage methods that incorporates the environmental conditions that each sample was subjected to prior to collection.

Molecular Analyses – Sage-Grouse Nests

We successfully detected common sage-grouse nest predators from predated sage-grouse nests via our molecular analyses. Coyotes were the dominant nest predator among our 5 study sites and corvids were the second most common nest predator. One of our five sites had higher corvid densities than the other four sites (based on three years of point-count survey data; C. Conway, unpublished data). Our molecular results indicated a higher proportion of corvid predations at the site with higher corvid densities which further supports the efficacy of our molecular technique for identifying nest predators. We detected a higher proportion of coyotes than other sage-grouse nest predation studies have reported (Coates et al. 2008, Lockyer et al. 2013, Taylor et al. 2017), and this difference may reflect one or more of the following reasons: 1) our study sites were remote with little human development and thus, may have lower corvid abundance (i.e., fewer anthropogenic subsidies for foraging and nesting; Leu et al. 2008), 2) coyotes may leave more DNA on eggshell remains compared to other mammalian and avian nest predators thus, increasing our detection rates for coyotes, or 3) past studies that relied on cameras at nests may have overestimated the proportion of corvid nest predators if the presence of a camera at a nest increases a corvid's ability to locate a nest (more so than for coyotes). We had several nests where multiple nest predators were detected and most of these "double" detections (n = 15) included an avian and mammalian species. Unfortunately, our molecular analyses cannot determine which species initially predated those nests, but our results suggest that scavenging eggs or eggshells from a predated nest may be a common event that is not always captured via cameras deployed at nests. Of the 18 nests that detected >1 predator species, 10 of those nests detected the predators on multiple samples (i.e., DNA was detected from multiple eggs). Thus, we feel confident that our molecular analysis is indeed capturing scavenging events. Lastly, this is the first study to report evidence that a cougar predated a sage-grouse nest and we plan to confirm this result via a DNA sequence analysis.

Detection of nest predator DNA via our molecular analysis was far lower for sage-grouse nests when evaluated by nest and sample (67% and 34%, respectively) when compared to our proof-of-concept study on artificial nests (95% and 73%). Similar to our proof-of-concept study, detection was higher when evaluated by nest, further re-enforcing that collecting multiple eggshell samples from predated nests increases success rates for

identifying predators via molecular techniques. Lower detection for sage-grouse nests (relative to our artificial nests) may have occurred because final survey intervals for sage-grouse nests ranged from 1–10 days whereas we collected samples from artificial nests within 2 days of a predation event (except for one artificial nest where a 1-week gap occurred between the predation event and sample collection). We did not find a relationship between final survey interval length or weather on DNA detection, but both time and environmental conditions influence DNA degradation (Murphy et al. 2007, DeMay et al. 2013, Barnes and Turner 2016). Thus, getting to samples quickly (i.e., within 1–2 days of a predation event) when collecting low-quality DNA such as saliva on eggshells would likely increase detection. Logistically, this can be challenging and may be one potential drawback to utilizing molecular techniques to identify nest predators based on eggshell remains at sage-grouse nests. Regardless, the number of sage-grouse nests where we detected predator DNA (n = 76) is comparable to studies utilizing cameras to identify nest predators (Staller et al. 2005, Coates and Delehanty 2010, Lyons et al. 2015, Burr et al. 2017, Guppy et al. 2017, Ellis et al. 2018), and many such studies do not explicitly report detection metrics (e.g., the number of cameras at predated nests that did not detect the nest predator) and/or camera malfunctions. Thus, results from our sage-grouse nests, in conjunction with our proof-of-concept results, provide evidence that molecular techniques provide a viable alternative method for determining predator-specific nest mortality (which can be used alone or in combination with nest cameras), and this method is especially useful for species where nest fate (and predator-specific nest predation) may be influenced by deploying cameras at nests.

Lastly, we were unable to collect samples from 32 predated sage-grouse nests because eggshell remains were not present at the nest site. Recent studies have highlighted the ability of molecular techniques for identifying species from low-quality environmental DNA (eDNA; e.g., identifying species from eDNA collected from soil; Leempoel et al. 2020). We suggest exploring the efficacy of using eDNA samples collected from nest sites (e.g., collecting dirt from in and around the nest bowl) as a means of identifying nest predators when eggshell remains are not present. Getting to predated nests more quickly than we did (i.e., within 1-2 days) would also likely reduce the percentage of predated nests without eggshell fragments.

Predator-Specific Mortality

Determining predator-specific mortality plays a critical role in elucidating how ecological gradients, disturbance, and land use influence patterns of predation and the role specific predators play in prey population dynamics (Griffin et al. 2011, Apps et al. 2013, Lyons et al. 2015). We predicted that increased canopy cover would reduce the probability of corvid predation due to increased aerial concealment whereas lateral concealment at a nest site would reduce the probability of mammalian predators. Our results indicate that higher shrub canopy cover decreases nest predation by coyotes (Fig. 1.2). Coyote habitat use and movement is closely tied to prey availability and foraging success (Gese et al. 1996, Moorcroft et al. 2006, Brunet et al. 2023). Coyotes may avoid areas of high shrub canopy cover because they are a coursing predator and higher shrub canopy cover could reduce their ability to efficiently navigate the landscape in search of prey. Further, coyotes may avoid areas of higher shrub canopy cover because high shrub canopy cover reduces prey detection by reducing visibility and the permeation of smells throughout the environment and thus, foraging success could be less efficient for coyotes in areas of high shrub canopy cover. Several studies have corroborated the positive relationship between of shrub canopy cover and nest survival in sage-grouse (Kolada et al. 2009, Webb et al. 2012, Lockyer et al. 2015), however, our study is the first to highlight a mechanistic link between shrub canopy cover and coyote-specific nest predation risk. Current sage-grouse management guidelines recommend maintaining 15–25% sagebrush canopy cover on breeding habitat (Connelly et al. 2000). Yet, our results suggest that in regions where coyotes are the primary nest predator, maintaining large tracks of land with >25% sagebrush canopy cover would improve sage-grouse nest success (Fig. 1.2). Thus, our results emphasize the importance of accounting for predator-specific nest mortality when making management decisions regarding sage-grouse habitat. Shrub canopy cover was also negatively associated with the probability of corvid predation (albeit not as strong as the relationship with the probability of coyote predation; Fig. 1.2), indicating that shrub canopy cover may be an important landscape characteristic for reducing nest predation for both avian and mammalian nest predators of sage-grouse nests. Confidence intervals overlapped 0 for the effect of shrub canopy cover on the probability of corvid predation, but our sample size was small for nests predated by corvids. We also found a negative relationship between average minimum temperature and the probability of nest

predation by both corvids and coyotes (Fig. 1.2). Incubating hens may increase the number of recesses (i.e., foraging bouts) they take during cold weather (Conway and Martin 2000a), and increased frequency of nest recesses can increase detection of nests by predators (Conway and Martin 2000b). Providing micro-habitat features that buffer against periods of low temperatures and/or providing high-quality forage near nests to reduce hen movement and bolster body condition during low temperatures could promote nest success in some regions. Our results also suggested a positive relationship between distance to a perennial water source and the probability of corvid predation. This positive relationship likely occurred because most of the corvid predations (58%) occurred at one study site with relatively few perennial water sources located near our surveyed nests (i.e., all surveyed nests at that study site were >3500-m from a perennial water source). We did not include study site as a fixed factor in our models because of model convergence issues and because we were interested in factors that influence predator-specific nest predation that were ubiquitous rather than site-specific effects. We predicted distance to water would have a stronger and negative relationship with the probability of mammalian predation because free water sources in dry environments are frequented by mammalian carnivores and can influence carnivore distributions and space use (Abade et al. 2014, Kluever et al. 2017). As predicted, distance to perennial water source had a negative relationship with the probability of coyote predation, but CIs overlapped 0. Lastly, variables associated with grazing were not included in any of our top models and thus, our results did not support a key prediction of the numerical response hypothesis (i.e., the probability of mammalian nest predation on sage-grouse nests will be lower on pastures with concurrent livestock grazing). However, our relatively small sample size of nests predated by corvids (n = 12) likely limited our ability to distinguish habitat characteristics and land use activities that influence the probability of corvid predation. Further, we had relatively few predated and successful nests in which cattle were present during the final survey interval or shortly thereafter (n = 9 and n = 21, respectively). Of those nine predated nests, eight detected coyote as the nest predator via our molecular analysis. Thus, we likely had too few nests to determine the effects of grazing on predator-specific mortality. The relationships were consistent among our top models and the averaged models (e.g., a negative relationship between shrub canopy cover and the probability of coyote predation), which provides confidence in the rigor of these relationships. Despite no

evidence for the numerical response hypothesis, our study provides a framework for implementing an effective, non-invasive method for identifying sage-grouse nest predators that can be used to better understand how management actions at a local and regional scale may impact an important component of sage-grouse recruitment.

Variation in the functional traits and foraging methods of predators as well as how ecological gradients and disturbance influence predator-specific patterns of nest predation gives rise to challenges when quantifying predator-prey relationships. Nest predation can influence population dynamics for many avian species and nest predator guilds can span taxonomic classes in many predator-prey communities. Moreover, factors that influence nest fate likely vary by predator species and/or functional groups. Despite this, efforts to identify factors that influence nest fate often group predation events across predators resulting in binary analyses of failed versus successful nests (i.e., regardless of the nest predator(s) responsible). This approach risks confounding or even negating important habitat and nest-site characteristics that may influence the probability that specific predators predate a nest. Deploying cameras at nest sites to identify the explicit predators responsible for nest predation has highlighted the spatial variation in predator-specific patterns of nest mortality. However, deploying cameras at nests is invasive and may affect nest fate in some species or ecosystems (i.e., they may bias the explicit metric they are intended to measure). The use of non-invasive molecular methods to identify predators of bird nests presents a novel opportunity to mitigate the challenges of both identifying the predator species responsible for nest predation events and quantifying factors that influence nest fate (which may vary among predator species) with a method that does not affect predator behavior or probability of nest detection.

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Table 1.1. Variables considered in our suite of candidate models evaluating factors that influence predator-specific mortality of sage-grouse nests in Idaho. Variables in bold font are those included in the global model after eliminating correlated variables, redundancy in functional relationships, and optimizing scales of effect.

Variable	Source
Average Minimum Temperature During the Final Survey Interval	PRISM Climate Group
Average Maximum Temperature During the Final Survey Interval	PRISM Climate Group
Average Mean Temperature During the Final Survey Interval	PRISM Climate Group
Average Precipitation During the Final Survey Interval	PRISM Climate Group
Average Max Height of Grass	Conway et al. (2019)
Average Height of Grass Leaf	Conway et al. (2019)
Average of Grass Amount Removed (i.e., Grazed)	Conway et al. (2019)
Average Effective Height of Grass	Conway et al. (2019)
Percent Aerial Concealment at the Nest Shrub	Conway et al. (2019)
Average Percent Horizontal Concealment at the Nest Shrub	Conway et al. (2019)
Shrub Canopy Cover at the Nest Site (900-m Scale)	Conway et al. (2019)
Shrub Canopy Cover (8-km, 14-km, 22-km, and 44-km Scales)	Rigge et al. 2021
Days Since Last Grazed	Conway et al. (2019)
Number of New Cattle Fecal Droppings	Conway et al. (2019)
Number of Old Cattle Fecal Droppings	Conway et al. (2019)
Distance to Fence	BLM 2022, Collected via surveys
Distance to Road	Idaho Roads 2019, Collected via surveys
Distance to Perching Structure	Collected via surveys
Distance to Agriculture	Dewitz and USGS 2021
Distance to Perennial Water Source	USGS 2017
Distance to Ephemeral Water Source	USGS 2017, Collected via surveys
Distance to Perennial or Epehmeral Water Source	USGS 2017, Collected via surveys
Distance to Nesting Structures (e.g., trees or cliffs)	USGS 2016, NLCD 2021, Collected via surveys
Distance to Powerlines	HIFLD 2022, Collected via surveys

Table 1.2. Comparison of species-specific detections from trail cameras (column 1) and our molecular analysis (column 2 – 6) for the proof-of-concept study summarized across 35 nests that detected DNA. Asterisks (*) indicate nests in which the species captured via trail camera was detected by our molecular analysis as well as a different species that was not captured via trail camera. Other species (column 6) include (from top down) a badger (*Taxidea taxus*) and a bobcat (*Lynx rufus*).

	Molecular Analysis				
	Raven/Crow	**Magpie**	**Raven & Magpie**	**Coyote**	**Other**
Raven	12	2	0	0	0
Magpie	1*	16****	0	2**	1*
Raven & Magpie	0	1	2	0	0
Coyote	1*	0	0	2**	1*

Table 1.3. Comparison of species-specific detections from trail cameras (column 1) and our molecular analysis (column 2 – 6) for the proof-of-concept study summarized across 86 samples that detected DNA collected from the 35 artificial nests (1 – 8 samples per artificial nest) that captured predation. Asterisks (*) indicate a sample in which the species captured via trail camera was detected by our molecular analysis as well as a different species that was not captured via trail camera. Other species (column 6) include (from top down) a badger (*Taxidea taxus*) and a bobcat (*Lynx rufus*).

	Molecular Analysis				
	Raven/Crow	**Magpie**	**Raven & Magpie**	**Coyote**	**Other**
Raven	29	2	0	0	0
Magpie	1	39****	1*	2**	1*
Raven & Magpie	3	2	2	0	0
Coyote	4**	0	0	5**	1

Table 1.4. Number of nest predator species detected (column 1) from predated sage-grouse nests and samples (columns 2 & 4) and the proportion of nests and samples each species was detected at (columns 3 & 5). If nests or samples detected more than one nest predator species, each species was assigned a proportion of the total number of species detected. If a coyote and magpie were detected at an individual nest, each species was assigned 0.5 for the number of nests it had been detected at. If that same detection came from a single sample, each species was assigned 0.5 for the number of samples it was detected at).

Species Detected	Number of Nests	Proportion of Nests	Number of Samples	Proportion of Samples
Coyote	47.33	62.28	126	62.69
Raven/Crow	20.33	26.75	46.5	23.13
Magpie	4.5	5.92	22	10.95
Badger	2	2.63	2	1.00
Bobcat	0.83	1.09	1	0.50
Red Fox	0.5	0.66	0.5	0.25
Cougar	0.5	0.66	3	1.49

Table 1.5. Species detections by sample for the 18 sage-grouse nests that our molecular analysis detected >1 predator species.

Nest ID	Total Samples	Raven/Crow	Magpie	Coyote	Bobcat	Cougar	Fox
F5209N1_20	7	4	-	4	-	-	-
F5224N2_21	5	-	5	2	-	-	-
F5232N1_21	8	3	2	-	-	-	-
F5242N1_21	8	-	3	2	-	-	-
F5437N1_20	6	1	-	1	1	-	-
FX0039N1_21	4	1	-	2	-	-	-
FX0138N1_20	10	-	-	1	1	-	-
FX0384N1_21	5	5	-	-	-	-	1
FX0431N1_21	9	1	-	5	-	-	-
FX0605N1_20	5	1	-	2	-	-	-
FX0608N1_21	4	1	-	2	-	-	-
FX0694N1_21	8	-	6	2	-	-	-
FX0697N1_20	8	3	-	4	-	-	-
FX0890N1_21	8	-	2	5	-	-	-
PAVAN1N1_20	9	2	-	1	-	-	-
SHCR4N1_20	6	2	-	-	-	3	-
FX0623N2_20	5	1	-	3	-	-	-
FX0623N2_20	9	3	-	1	-	-	-

Table 1.6. Top models (delta $AIC_c < 2$) evaluating detection of predator species via our molecular analysis by nest as a function of survey interval, temperature, precipitation, and total samples collected. The asterisk (*) indicates an interaction term between total precipitation and average minimum temperature during the final survey interval.

Intercept	Survey Interval Length	Precip.	Min. Temp.	Total Samples	Precip. * Min. Temp.	df	logLik	AIC_c	ΔAIC_c	*w*
-0.29						1	-70.30	142.64	0.00	0.16
-0.30	0.34		0.32			3	-68.41	143.05	0.42	0.13
-0.30	0.25					2	-69.53	143.19	0.55	0.12
-0.30			0.22			2	-69.67	143.47	0.83	0.10
-0.29				-0.12		2	-70.11	144.34	1.71	0.07

Table 1.7. Top models (delta $AIC_c < 2$) evaluating detection of predator species via our molecular analysis by eggshell sample as a function of survey interval, temperature, and precipitation.

Intercept	Survey Interval Length	Precip.	Max. Temp.	Min. Temp.	Precip. * Min. Temp.	df	logLik	AIC_c	ΔAIC_c	*w*
-0.66						1	-358.30	718.61	0.00	0.22
-0.67			0.09			2	-357.78	719.59	0.99	0.14
-0.66				0.06		2	-358.06	720.14	1.53	0.10
-0.66		-0.03				2	-358.23	720.49	1.89	0.09
-0.66	-0.02					2	-358.28	720.58	1.97	0.08

Table 1.8. Top models (delta $AIC_c < 2$) evaluating factors that influence predator-specific nest mortality of sage-grouse nests. The plus signs (+) indicate covariates included in the top models with a $\Delta AIC_c < 2$. The table does not include all covariates evaluated in the analysis.

Percent Lateral Cover	Dist. to Perch	Dist. to Perennial Water Source	Precip.	Percent Shrub Cover	Avg. Min. Temp.	df	logLik	AICc	ΔAIC_c	*w*
	+	+		+	+	10	-103.80	229.15	0	0.04
	+	+	+	+	+	12	-101.97	230.19	1.04	0.03
+	+	+		+	+	12	-102.20	230.60	1.44	0.02

Figure 1.1. The locations of our 5 study sites (black circles) in Idaho, USA.

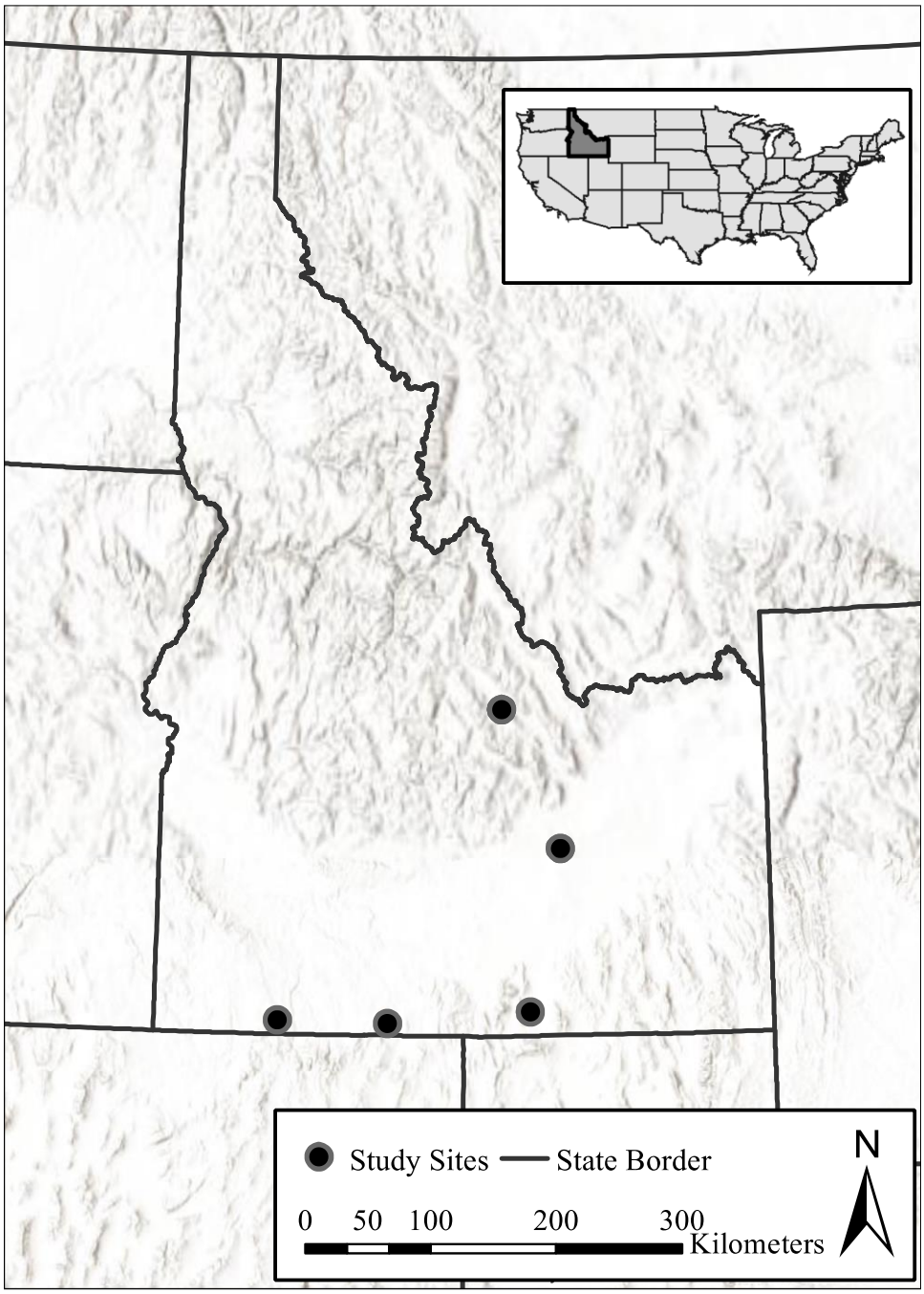
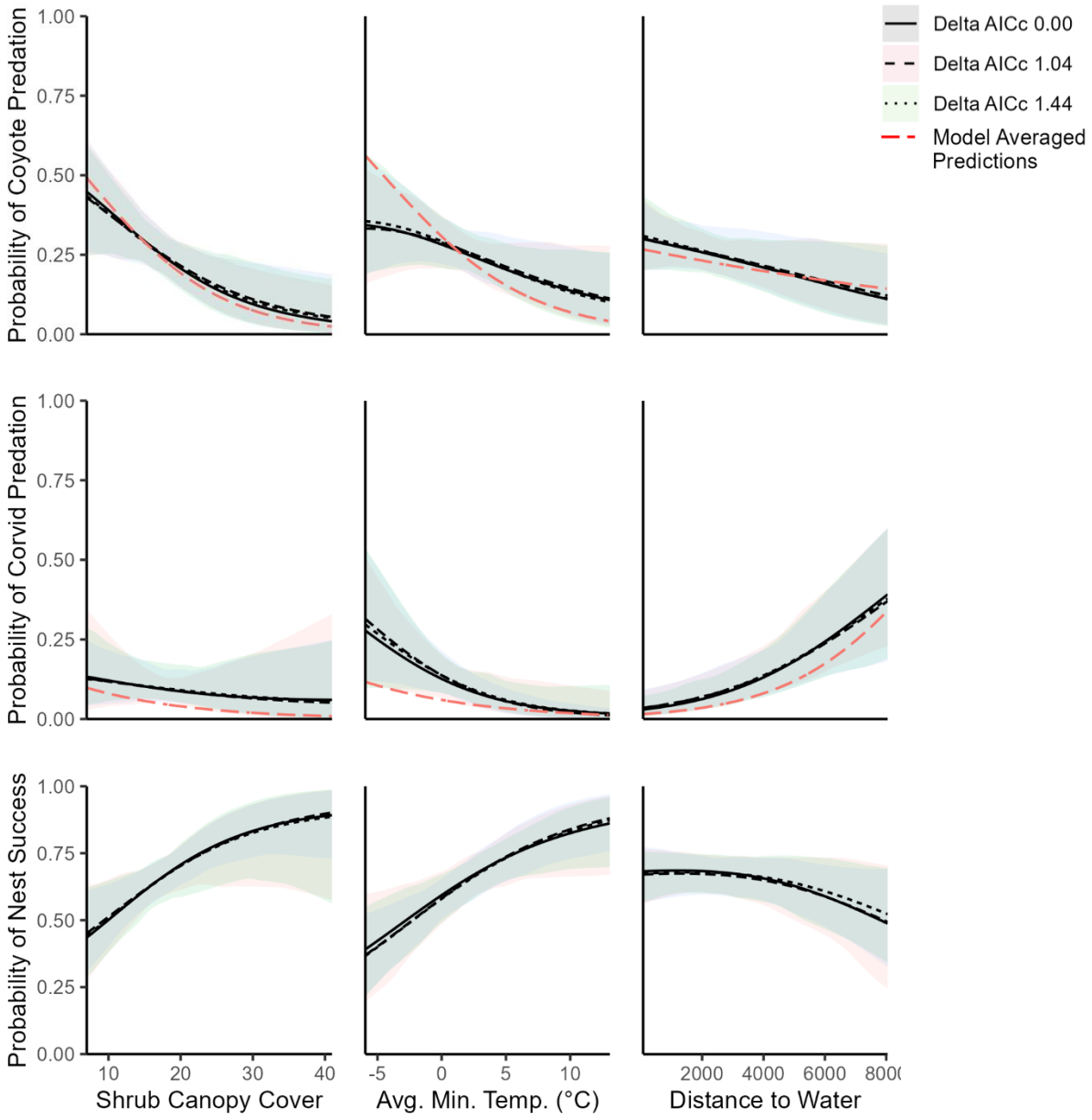


Figure 1.2. Partial effects plots for response variables in the top models evaluating factors that influence predator-specific nest mortality with confidence intervals that did not overlap 0. The black lines represent the relationship between the covariate and the response variables for the 3 top models with a ΔAIC_c <2. The dashed red lines show the relationship between the covariates and the coyote and corvid response variables averaged across all models that encompassed 95% of the model weight.



Chapter 2: Where's the Beef? The Influence of Grazing on the Spatiotemporal Activity Patterns of a Primary Sage-Grouse Nest Predator

INTRODUCTION

Human activities have had a myriad of effects on wildlife communities (Vitousek et al. 1997). While land conversion and over-exploitation are arguably the most salient ways that humans impact wildlife (Maxwell et al. 2016, Caro et al. 2022), recreation and socioeconomic activities that are often assumed to be sustainable can also adversely affect wildlife communities (Frid and Dill 2002, Taylor and Knight 2003, Shannon et al. 2017). Animals often perceive humans and human-related activities as a risk and respond by increasing anti-predator behaviors (e.g., increased vigilance or fleeing) that are metabolically and physiologically costly (Frid and Dill 2002). Increases in anti-predator behavior can reduce energy intake and increase stress and thereby impact body condition, survival, and reproductive output (Frid and Dill 2002, Müllner et al. 2004, Naylor et al. 2009, French et al. 2011). Further, animals often partition themselves in space or time to avoid the perceived (or real) risk of human activity resulting in perturbations of key ecological processes that shape the structure and function of wildlife communities (e.g., predator-prey interactions; Frid and Dill 2002, Gaynor et al. 2018). Thus, documenting the effects of human activities on animal behavior and spatiotemporal activity patterns can be critical for ensuring that human activities are compatible with persistence of wildlife populations.

Perturbations in predator-prey interactions as a result of human activity can have cascading effects across trophic levels. For example, cougars (*Puma concolor*) avoided high-use areas by tourists in Utah which subsequently impacted the age structure of cottonwood trees due to increased mule deer (*Odocoileus hemionus*) populations (Ripple and Beschta 2006). Similarly, coyotes (*Canis latrans*) in Colorado avoided areas with high human use creating a "human-shield" (i.e., refugia from predation; Berger 2007) for mule deer and consequently, reduced recruitment of herbaceous forage in those areas (Waser et al. 2014). Human activity can also alter predator-prey interactions by influencing diel activity patterns of both predator and prey (Gaynor et al. 2018). Human disturbance shifted diel activity patterns of several predator and prey species in Africa which altered temporal overlap among

species and thus, predator access to prey (Mills and Harris 2020). Understanding when and how human activity alters key ecological processes via changes in spatiotemporal activity patterns of animals is an important step in reducing human-wildlife conflicts and maintaining well-functioning ecological communities.

Domestic livestock grazing is common throughout the sagebrush steppe in western North America (Veblen et al. 2014). Efforts to ensure that grazing practices are sustainable and do not adversely affect greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) have resulted in grazing management guidelines for rangelands throughout the western U.S. (USFWS 2013). Despite reductions in livestock grazing intensity over the past 50 years, sage-grouse populations have continued to decline across their range (Borman 2005, Coates et al. 2022). Sage-grouse population growth is particularly sensitive to changes in nest success (Taylor et al. 2012), and many activities proposed to cause sage-grouse population declines are thought to do so via increased nest predation (Beck and Mitchell 2000, Knick and Connelly 2011, Webb et al. 2012). Domestic cattle (*Bos taurus*) grazing is assumed to influence sage-grouse nest success by reducing grass height which reduces nest concealment and, consequently, facilitates nest detection by predators (hereafter the reduced concealment hypothesis; Beck and Mitchell 2000). Grass height influences nest success at the nest-site scale (Doherty et al. 2014) and grass height is typically lower in grazed pastures (Doherty et al. 2014, Smith et al. 2018). Yet, nest success is similar among pastures with varying grazing intensities (Smith et al. 2018). Given that lower grass height is associated with higher nest predation rates at the local nest-site scale, why then isn't nest success lower in pastures with higher grazing intensity? To ensure that domestic cattle grazing is compatible with persistence of sage-grouse populations, we need to evaluate explicit mechanisms by which grazing could affect sage-grouse nest success.

One possible explanation for these apparently conflicting patterns at the nest-site and pasture scale regarding the relationship between livestock grazing and sage-grouse nest success involves a localized numerical response by one or more primary sage-grouse nest predators. A temporary, local reduction in the number of predators in response to the presence of cattle (hereafter the numerical response hypothesis) could offset the effects of the reduced concealment hypothesis. That is, some sage-grouse nest predators might avoid cattle

due to historical persecution by humans resulting in a localized numerical response. Hence, similar nest success on both grazed and non-grazed pastures could occur if both the numerical response and reduced concealment hypotheses were occurring concurrently. The numerical response hypothesis predicts that one or more nest predator species avoid cattle by partitioning themselves in space and thus, are unavailable to consume sage-grouse nests on pastures with cattle. Additionally, the effects of the reduced concealment hypothesis could also be offset if one or more nest predators partition themselves temporally to avoid cattle. Altering diel activity patterns could result in increased nest predator activity during portions of the day when they are less efficient at locating sage-grouse nests. To test the numerical response hypothesis, we evaluated whether coyotes, a primary sage-grouse nest predator, avoided cattle by altering space use (as predicted by the numerical response hypothesis) as well as whether coyotes shifted diel activity patterns in response to the presence of cattle.

METHODS

Study Sites

We collected field data at two study sites in southeastern Idaho (Fig. 2.1). The predominant overstory at both study sites was Wyoming big sagebrush (*Artemisia tridentata wyomingensis*; Conway et al. 2018). The predominant understory at the study sites included Sandberg bluegrass (*Poa secunda*), bottlebrush squirreltail (*Elymus elymoides*), bluebunch wheatgrass (*Pseudoroegneria spicata*), western wheatgrass (*Pascopyrum smithii*), and needlegrass (*Achnatherum* spp and *Hesperostipa* spp; Conway et al. 2018). Based on molecular analyses of predated sage-grouse nests (Chapter 1), coyotes were the primary sage-grouse nest predator at both study sites. Other potential nest predators at the study sites included American badger (*Taxidea taxus*), corvids (*Corvus corax, C. brachyrhynchos,* and *Pica hudsonia*), red fox (*Vulpes vulpes*), and bobcat (*Lynx rufus*). Each study site consisted of several fenced pastures that were managed for livestock grazing. The fences surrounding the pastures were designed to keep cattle in (or out) but were permeable to potential nest predators. Both study sites were on land managed by the U.S. Bureau of Land Management and this agency leases the land to permittees who own cattle and graze the pastures based on grazing guidelines that restrict the intensity, timing, and frequency of grazing.

Data Collection

We deployed 104 trail cameras (Reconyx PC900, Reconyx HC600, and Cuddeback 20mp White Series) across 6 fenced pastures during May – July 2021. Grazing was scheduled to occur for at least 30 days in the pastures during camera deployment. Sizes of the 6 pastures ranged from 23-km^2 – 30-km^2. We used ArcGIS (ESRI 2021) to overlay 1-km^2 grid cells with the pasture boundaries. We deployed a single camera per grid cell and placed each camera on a movement corridor (e.g., fence lines, game trails, 2-track roads) closest to the center of the grid cell. We placed the camera at the cell center of 6 grid cells because we were unable to find movement corridors within a grid cell. Camera type (i.e., Reconyx or Cuddeback) was randomly assigned to locations in each pasture, however, an equal number of each camera type was used (or nearly equal if the number of locations was an odd number). We set cameras to take a burst of 5 photos with 1-5 second delay between photos (1-5 sec was the minimum delay possible which differed depending on camera type; see above). We attached cameras to t-posts or large sagebrush branches. We camouflaged t-posts and cameras with sagebrush branches and grass when they were attached to t-posts that were not part of a fence line. We used TimeLapse2 (Greenberg 2020) to visually process photos and record detection events. We recorded all species detected via cameras including wildlife, humans, cattle, and other domestic animals.

Coyote Space Use

We used an occupancy modeling framework (MacKenzie et al. 2017) to evaluate how the presence of cattle influenced the relative frequency of use by coyotes at camera sites. Occupancy models are hierarchical models consisting of two sub-models (Eq. 2.1): an occupancy sub-model (i.e., occupancy probability) and a detection sub-model (i.e., detection probability). Occupancy models were designed to estimate the probability of occupancy at discrete, independent sites where the occupancy status (i.e., occupied or not) of a site is assumed constant throughout sampling periods (MacKenzie et al. 2017). Each camera trap monitors a small portion of the landscape (i.e., the viewshed of the camera) and the detection of an animal is conditional on both the camera being deployed within an animal's home range and the animal crossing the viewshed of the camera (Burton et al. 2015, Hofmeester et al. 2019). Camera trap data inherently violate a major assumption of occupancy models

because the viewshed of a camera does not remain in the same status (occupied versus not occupied) throughout a sampling period (Burton et al. 2015, MacKenzie et al. 2017, Hofmeester et al. 2019). Consequently, the probability of detecting an animal (detection probability) equates to the probability that an animal uses the area in front of the camera given that the animal is available for detection (i.e., the home range of the animal overlaps the camera; Burton et al. 2015, Hofmeester et al. 2019). Thus, we leveraged the hierarchical structure of occupancy models and used the R (R Core Team 2023) package *unmarked* (Fiske and Chandler 2011) to evaluate whether the presence of cattle influenced the probability a camera site was used by coyotes while controlling for factors that influence the distribution of coyote home ranges across the landscape. Our sampling periods consisted of each 24-hour period the camera was deployed and operational. Covariates in the detection sub-model included the sum of cattle detections per sampling period at each camera site (i.e., daily cattle detections) and camera type (i.e., Reconyx or Cuddeback). Cattle often travel in herds which can result in many detections occurring over long periods of time. Therefore, we considered a detection event as independent from other events if 30-minutes passed between two detections. We included camera type in the detection sub-model because trigger speed and the distance from a camera in which an animal will be detected can vary among camera types. We controlled for factors that might influence the distribution of coyote home ranges across the landscape by including average shrub canopy cover (Rigge et al. 2021) at a 44-km^2 scale (the average size of coyote home ranges in our system; Hernendez and Laundre 2003), average herbaceous cover at a 44-km^2 scale (Rigge et al. 2021), distance to the nearest perennial water source (USGS 2017), and distance to agricultural land (Dewitz and USGS 2021) in the occupancy sub-model. We included distance to agricultural land because the nearest developed land to any of the 6 pastures was agricultural land. We accounted for survey effort per camera site by excluding the date ranges when cameras were nonoperational (e.g., if a camera was knocked over for a portion of sampling periods) from the analysis. We standardized all continuous variables by subtracting the mean and dividing by the standard deviation. We compared all subsets of our global detection sub-model (i.e., summation of cattle detections per sampling period and camera type) while maintaining an intercept-only occupancy sub-model. We selected a top detection sub-model based on Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and

Anderson 2002). We then compared all subsets of our global occupancy sub-model (i.e., shrub canopy cover, herbaceous cover, distance to water, and distance to agricultural land) while incorporating the top detection sub-model. We selected a top occupancy model based on AIC_c.

Coyote Diel Activity Patterns

We used the *overlap* package (Meredith and Ridout 2020) in program R (R Core Team 2023) to evaluate whether coyotes altered their diel activity patterns when cattle were present. Using the timestamps from trail cameras, package *overlap* estimates daily activity patterns during a 24-hour period nonparametrically using kernel density estimates (Ridout and Linkie 2009). Temporal overlap (Δ) is estimated by quantifying the minimum area under two kernel density estimates, with an overlap coefficient of 1 being complete temporal overlap and 0 being no temporal overlap (Ridout and Linkie 2009). We quantified the amount of temporal overlap between diel activity patterns of coyotes when cattle were present and diel activity patterns of coyotes when cattle were not present. We considered consecutive coyote detections on the same camera to be independent based on ≥30-minute intervals (i.e., a detection was considered independent if 30 minutes separated two detections). We partitioned coyote detections into two groups: 1) Coyote detections that occurred prior to any cattle detections at a camera site and coyote detections that occurred after the last cattle detection at a camera site (i.e., cattle absent), and 2) coyote detections that occurred in between the first and last cattle detection at a camera site (i.e., cattle present). We converted the timestamps of cameras to radial time and scaled the time of day to sunrise and sunset to account for changes in day length because activity time across a 24-hour period is circular and the non-parametric probability densities are often bimodal for wildlife (Nouvellet et al. 2012, Meredith and Ridout 2020). We used the Δ_4 estimator to estimate the coefficient of overlap because our sample size was ≥50 detections for coyotes both when cattle were present and when cattle were absent (Meredith and Ridout 2020). We used 10,000 smoothed bootstrap samples to estimate the basic 95% confidence intervals (Meredith and Ridout 2020). We also used the methods described above to quantify the amount of overlap between diel activity patterns of cattle and coyotes at cameras where both species were detected.

RESULTS

Coyote Space Use

We had 95 cameras operational for one or more 24-hour sampling periods resulting in 6,230 total sampling periods for our space use analysis. Domestic cattle or wildlife knocked over 21% of the 95 cameras at some point during deployment. We detected cattle on ≥1 occasion at 86% of the cameras (*n* = 82 of 95 cameras) and had 3,291 independent cattle detections. Daily counts of independent cattle detections at camera sites with ≥1 detection ranged from 1 – 18 cattle detections. We detected coyotes on ≥1 occasion at 74% of the cameras (*n* = 70 of 95 cameras) across 257 of the sampling periods. The top detection sub-model included daily cattle detections at camera sites and camera type (Table 2.1a). The top occupancy model which incorporated the top detection sub-model (i.e., daily cattle detections and camera type) included average percent canopy cover, percent herbaceous cover, and distance to perennial water source (Table 2.1b). The number of cattle detections per sampling period at camera sites was positively associated with coyote use (Fig. 2.2; beta = 0.22, 95% CI = 0.14 – 0.30) and coyote detections were higher using Reconyx cameras (beta = 0.73, 95% CI = 0.45 – 1.01). All covariates included in the top occupancy sub-model had confidence intervals that overlapped 0. No other models had a ΔAIC_c <2.

Coyote Diel Activity Patterns

We removed an additional 7 cameras from the diel activity pattern analysis because their clocks appeared to be inaccurate. We had 162 coyote detections when cattle were present in the pastures and 113 coyote detections when cattle were absent in the pastures. We had 267 coyote detections and 3,096 cattle detections at cameras where both species were detected at least once throughout the sampling period for that camera site. The bootstrapped mean temporal overlap ($\overline{\Delta}$) of coyote diel activity patterns when cattle were present and when cattle were absent was 0.84 (range of $\overline{\Delta}$ = 0.81 – 0.93). Thus, the presence of cattle did not appear to influence the diel activity patterns of coyotes. Coyotes appeared to be primarily nocturnal in our system, but another peak in activity occurred in the afternoon (Fig. 2.3). The bootstrapped mean temporal overlap ($\overline{\Delta}$) of coyote and cattle diel activity patterns at cameras

where both species were detected was 0.616 (range of $\bar{\Delta}$ = 0.527 – 0.623). Cattle appeared to be active for most of the 24-hour period in our system (Fig. 2.4).

DISCUSSION

Coyote Space Use

Human activities can alter animal space use in ways that change predator-prey interactions and other key ecological processes (Ripple and Beschta 2006, Waser et al. 2014). Quantifying those effects is essential for developing effective management strategies where recreational and socioeconomic activities overlap with wildlife habitat. Our results indicate that coyotes do not partition themselves in space to avoid cattle. Our results did not support a key prediction of the numerical response hypothesis; the number of cattle detections at camera sites was positively (not negatively) associated with coyote use at camera sites. Thus, in our system, the relationship between sage-grouse nest success and livestock grazing is not explained by the numerical response hypothesis (at least not by coyotes, the primary sage-grouse nest predator in our system). Cattle tend to select for areas with higher-quality forage which may be associated with increased abundance and diversity of small mammals which are important prey for coyotes (Kelrick et al. 1986, Bailey 1995, Freeman et al. 2014). Increased prey availability in areas with high-quality forage may be a more powerful driver of coyote space use and outweigh any perceived risk coyotes associate with cattle. Regardless, our results highlight that a primary land use activity across the western U.S. (domestic livestock grazing) does not alter the fine scale (i.e., pasture level) space use patterns of an important predator species in the sagebrush steppe.

Coyote Diel Activity Patterns

Wildlife will often partition themselves in time to avoid human activities (Gaynor et al. 2018). Such shifts in diel activity patterns can affect interspecific interactions by altering the temporal overlap between species (Mills and Harris 2020). However, we did not find evidence that the presence of cattle shifted the diel activity patterns of coyotes. Therefore, in our system, the relationship between sage-grouse nest success and livestock grazing is not influenced by any temporal shifts in coyote diel activity patterns to portions of the day when they are less efficient at locating sage-grouse nests. The pastures in our system were small

relative to the average size of a coyote home range, and so multiple pastures likely overlap with the home range of a single coyote. Thus, coyotes may be altering diel activity patterns in response to the presence of cattle in adjacent pastures. That is, coyotes could be responding to the presence of cattle at a larger spatial scale and comparing diel activity patterns of coyotes on large tracks of sagebrush steppe where cattle are absent to where cattle are present is needed to better evaluate whether the presence of cattle induce a behavioral response by coyotes. Our results also indicate that cattle were active for most of the 24-hour period in our system, except for the hottest portions of the day (i.e., late afternoon; Fig. 2.4). For coyotes, the consequences of avoiding cattle by increasing activity time during the hottest portions of the day (e.g., thermoregulation and reduced prey activity; O'Farrell 1974, Lendrum et al. 2017) may outweigh any perceived risk that coyotes associate with cattle. Therefore, coyotes may be unable to avoid cattle temporally because cattle are active within some portion of their home range during most of the 24-hour period. Consequently, the temporal overlap of diel activity patterns between coyotes and prey species in our system will likely remain the same under current grazing strategies. The relatively low temporal overlap (0.616) between coyotes and cattle is likely an artifact of cattle being active during portions of the day when coyotes were inactive and not an indication of coyotes partitioning themselves in time to avoid cattle.

Sage-Grouse Management

Predation is the most common cause of sage-grouse nest failure (Moynahan et al. 2007), but surprisingly few studies have evaluated the effects of land use on the spatiotemporal activity patterns of key sage-grouse nest predators and the implications of those effects on sage-grouse nest success. At our study sites, coyotes did not adjust their space use or diel activity patterns based on the presence of cattle. If coyotes perceive cattle as a risk, they appear to make a trade-off between the potential risk of being around cattle for an alternative reward. Conversely, coyotes may simply not perceive cattle and the human activities associated with cattle as a risk. Either way, grazing is not increasing sage-grouse nest success via a temporary and local numerical reduction in a primary nest predator at our study sites (i.e., we found no support for the numerical response hypothesis in coyotes). One alternative hypothesis is that sage-grouse respond to grazing (i.e., the presence of cattle or

reduced grass height) by selecting areas within a pasture where grazing pressure is low (i.e., areas with “adequate” nest concealment). Sage-grouse are known to select nest sites away from areas perceived as risky (e.g., away from areas with high densities of avian predators; Dinkins 2012). Grazing intensity, duration, and timing are restricted at our study sites to align with sage-grouse management guidelines. Current grazing practices could result in areas of nesting refugia for sage-grouse within a pasture. Thus, grazing management guidelines (e.g., grazing practices that do not uniformly reduce nest concealment across an entire pasture) may play an important role in promoting sage-grouse nest success. Evaluating sage-grouse nesting behavior in response to cattle (e.g., do sage-grouse avoid nesting in areas of high cattle use?) will help further document the management options in areas that strive to maintain sage-grouse populations while also grazing domestic livestock.

Assumptions that certain land use activities increase sage-grouse nest predation via mechanisms like increased predator foraging efficiency, increased predator occurrence due to subsidies, and increased efficiency in predator movement are common (Dzialak et al. 2011, Doherty et al. 2014, LeBeau et al. 2014, Kirol et al. 2015). Assuming that the functional and numerical response of predators to land use are ubiquitous is not appropriate because predator composition, behavior, and foraging strategies can vary spatially, temporally, and among species within a predator guild (Lahti 2009). Providing managers with explicit mechanisms linking land use activities to sage-grouse demographics will better facilitate balancing land use with sage-grouse management at both local and regional scales.

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Equation 2.1. Occupancy models consist of two sub models: 1) an occupancy sub-model where *z* is the true occupancy state of site *i* and is governed by the random variable ψ (i.e., occupancy probability) drawn from a Bernoulli distribution, and 2) a detection sub-model where *y* is the probability of detecting a species at site *i* during the survey occasion *j* conditional on *z* (i.e., the occupancy status of site *i*).

$$z_i \sim Bernouli(\psi)$$

$$y_{ij} \sim Bernoulli(p_{ij}, z_i)$$

Table 2.1. Model selection tables evaluating coyote occupancy at camera sites. The top detection sub-model (a) was incorporated into the model selection process for the occupancy sub-model (b). Only occupancy sub-models with a ΔAIC_c <11 are shown here.

(a)

Intercept	Daily Cattle Detections	Camera Type	df	logLik	AIC_c	ΔAIC_c	*w*
-3.75	0.23	0.85	4	-1046.46	2101.37	0	0.99
-3.43		0.62	3	-1054.07	2114.39	13.03	0.00
-3.22	0.24		3	-1065.61	2137.48	36.11	0.00
-3.18			2	-1080.10	2164.33	62.97	0.00

(b)

Intercept	Herbaceous Cover	Shrub Cover	Dist. to Agriculture	Dist. to Water	df	logLik	AIC_c	ΔAIC_c	*w*
86.87	36.59	71.59		-11.9	7	-1032.99	2081.27	0	0.87
7.02	3.23	5.79			6	-1036.77	2086.50	5.23	0.06
7.23	3.48	6.00	-0.21		7	-1036.77	2088.83	7.56	0.02
5.18		3.39	2.50	-0.76	7	-1037.31	2089.91	8.64	0.01
5.18		3.39	2.50	-0.76	7	-1037.31	2089.91	8.64	0.01
4.08		2.73	1.95		6	-1038.51	2089.98	8.71	0.01
2.48	1.18				5	-1040.66	2092.00	10.73	0.00

Figure 2.1. The two study sites in southern Idaho (black circles): Pahsimeroi Valley and Big Butte.

Figure 2.2. Probability of coyote detection at camera sites as a function of daily cattle detections.

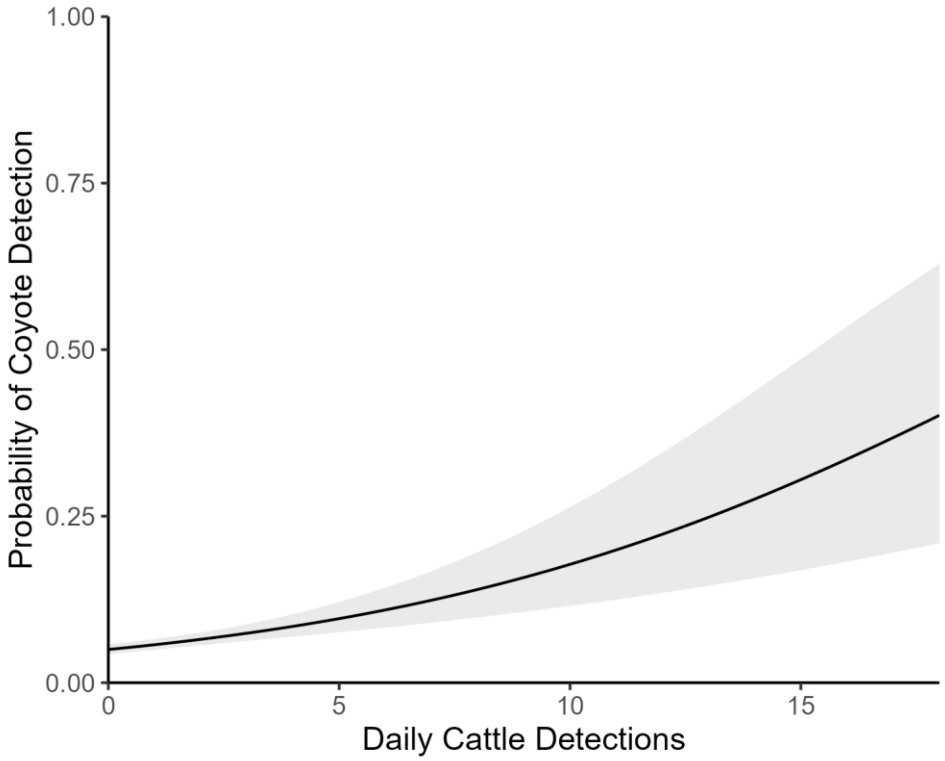

Figure 2.3. Non-parametric kernel density estimates of coyote diel activity patterns when cattle were present (dashed line) and when cattle were absent (solid line). The bootstrapped mean temporal overlap (i.e., the minimum area under both kernel density estimate; $\overline{\Delta}$) of coyote diel activity patterns when cattle were present and when cattle were absent was 0.84 (range of $\overline{\Delta}$ = 0.81 – 0.93).

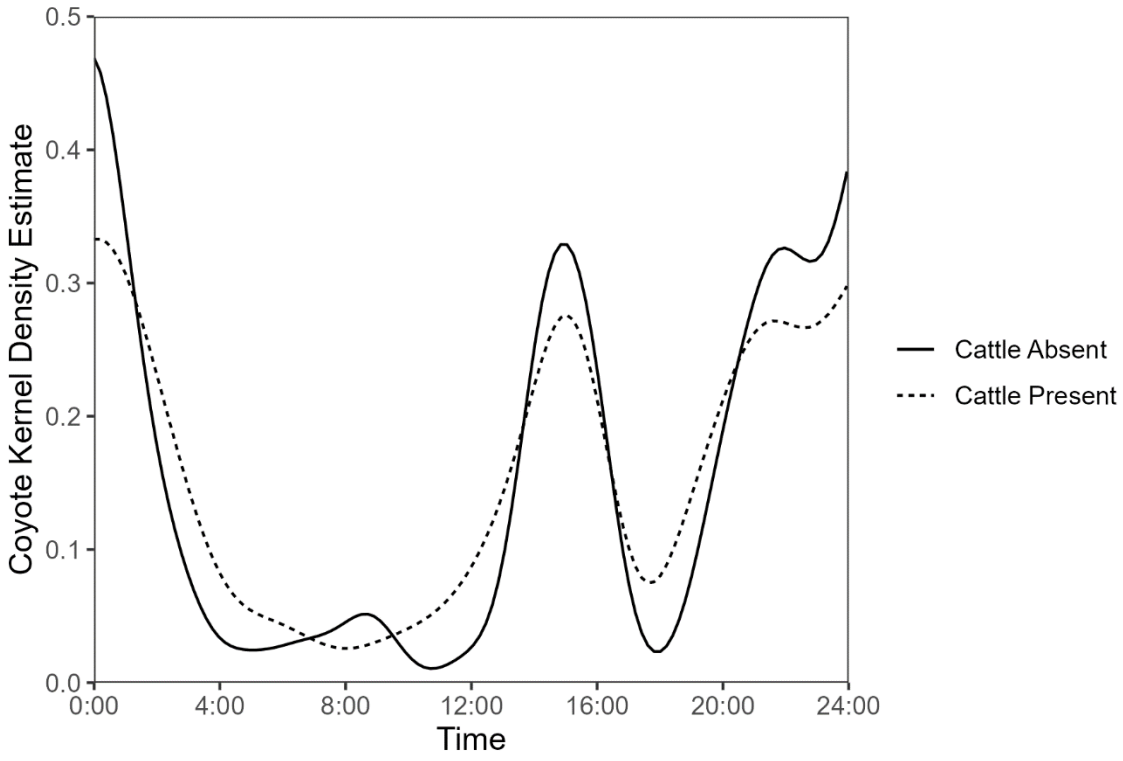

Figure 2.4. Non-parametric kernel density estimates of coyote diel activity patterns (dashed line) and cattle diel activity patterns (solid line) at trail camera sites where both species were detected. The bootstrapped mean temporal overlap (i.e., the minimum area under both kernel density estimates; $\overline{\Delta}$) of coyote diel activity patterns and cattle diel activity patterns was 0.616 (range of $\overline{\Delta}$ = 0.527 – 0.623).