Diverse apex predator guild impacts the foraging decisions of avian scavengers through carrion availability

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Abstract

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Scavengers are vital to maintaining ecosystem health by efficiently recycling and redistributing nutrients from carrion. However, increasing anthropogenic pressures have led to declines in many scavenger populations, particularly facultative scavengers such as large carnivores. There is limited understanding of how interactions between healthy populations of sympatric large carnivores structure foraging opportunities for scavengers through changes in the availability of carrion. In Chapter 1, I investigate how interference competition between two large carnivores, gray wolves (*Canis lupus*) and cougars (*Puma concolor*), alters the daily maximum counts and activity rates of avian scavengers at kill sites. Between 2021 – 2025, I gathered scavenger activity at 32 wolf and 27 cougar kills using direct observations and camera trapping. I found higher maximum counts of ravens, golden eagles, and bald eagles at wolf kills than at cougar kills, likely due to less-confrontational competition strategies used to limit the loss of biomass to scavengers. The subordinate status of magpies in the scavenger dominance hierarchy, along with their increased agility and heightened sense of smell, likely led to similar maximum counts at wolf and cougar kills. When wolves kleptoparasited cougar kills, there was an increase in the daily maximum counts of ravens, magpies, and golden eagles. This indicates that wolves assist scavengers in locating and accessing previously hidden and defended cougar kills. However, wolf presence only increased the

activity rates and, likely, the amount of biomass acquired for ravens and bald eagles. The activity rates of magpies and golden eagles did not increase as individuals remained for less time. In Chapter 2, I investigate whether territorial common ravens made movement decisions during the winter that were consistent with optimal foraging theory, given the availability of carrion associated wolf foraging and recreational human hunting. I tracked 18 ravens (12 female, 6 male) using GPS data loggers between 2019 – 2024, resulting in 1702 days, to determine their daily foraging destinations. I fit two binomial generalized linear mixed models to represent daily raven decision-making. The first model estimated the probability that a raven left its territory. The second model, conditional on the raven leaving its territory, estimated the probability that a raven visited the recreational hunting regions. Both models included covariates for food availability, such as wolf-kill availability and visits, as well as recreational hunting season and biomass. The models also included other covariates that may affect raven movement decision-making by altering input costs, such as commute distance and whether it was early or late winter, or by providing information about food availability, such as daily temperature, snow depth, and the movement decisions of conspecifics. Ravens generally behaved consistently with predictions from optimal foraging theory, with wolf-kill encounters decreasing the probability of seeking alternative foraging options in other locations, despite their low availability on the landscape. However, raven decisions were not affected by wolf kills within their territory when a visit was not recorded. When traveling outside of their territories, ravens had a greater probability of visiting recreational hunting regions on days within hunting season and when their commute was shorter. I found no evidence that ravens tracked fluctuations in biomass availability in recreational hunting areas and are instead informing movement on the timing of recreational hunting seasons. My findings suggest that ravens are making movement decisions based on immediate knowledge of the resources available to them, including those in distant locations.

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The work I have done here would have been impossible without the scientific community in Yellowstone: Matt Metz, Dave Haines, Kira Cassidy, Erin Stahler, Nikki Tatton, Chris Geremia, and the many technicians throughout the winters: Caleb Basa, Nick Peterson, Kole Meinhart, Ellie Mondloch, Louis Kreemer, Dylan Sanborn, Zoe Ward, and many more. Their tireless effort to put in the hours and miles gave me the opportunity to work with the best picture of a wolf population anywhere in the world.

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Chapter 1: Apex predator-scavenger dynamics in Yellowstone National Park

1.1 Introduction

Scavengers are vital to maintaining ecosystem health by efficiently recycling and redistributing nutrients from carrion (DeVault et al. 2003). Without their presence, the build-up of decaying carcasses can become breeding grounds for harmful bacteria and toxic compounds to both animal and human populations (Blandford et al. 2019, Lim et al. 2020, Santori et al. 2020). Abiotic functions such as water quality and greenhouse gas emissions are also regulated by the removal of carrion (Cabral 2010, Plaza and Lambertucci 2022). Despite their importance, a disproportionately large percentage of scavenging species have declining populations when compared with other vertebrates (Sonawane et al. 2025). Large predators that scavenge carrion, alternatively called apex scavengers, are disproportionately affected by many anthropogenic drivers of population decline (DeVault et al. 2003, Wilson and Wolkovich 2011, Sonawane et al. 2025). Additionally, temperate systems supporting multiple large carnivore population are less common and therefore, understudied. I take advantage of Yellowstone National Park, a system that has repopulated its top carnivores, creating an opportunity to better understand how scavengers benefit from multiple sources of carrion.

Yellowstone is an unparalleled location for research into the interactions between scavengers, large carnivores, and anthropogenic influences. Yellowstone exists as one of the few remaining reasonably intact temperate ecosystems with healthy populations of all native top carnivores (Noss et al. 2002) and a high carnivore density (Ripple et al. 2014). Thanks to its protected status, Yellowstone remains largely untouched yet is surrounded by various hotspots of human activity. Gateway communities continue developing to accommodate the massive numbers of park visitors passing through each year, which increased from 3.6 million to 4.7 million between 2010 and 2025 (https://irma.nps.gov/Stats/Reports/Park/YELL). These communities also provide alternative recreation opportunities such as hunting in the surrounding public lands.

Yellowstone did not always have healthy populations of predators, as gray wolves (*Canis lupus*) were extirpated in 1926 and cougar (*Puma concolor*) populations were suppressed to low numbers by the late 1930s (Ripple et al. 2022). In this time, the ecosystem changed drastically with elk populations

skyrocketing past carrying capacity in the absence of their native predator (Taper and Gogan 2002) and many riparian ecosystems converting to grassland in the face of over browsing (Hobbs et al. 2024). Eventually, the Endangered Species Act propelled the reintroduction efforts for gray wolves in 1995 alongside the natural recolonization by cougars following the removal of bounties and state-managed hunting quotas (Ruth et al. 2019, Ripple et al. 2022), creating a natural experiment that scientists have observed for over 30 years to investigate the recovery path and importance of these apex predators in this ecosystem.

Wolves in Yellowstone have played an integral role in stabilizing ecosystem processes through top-down effects like predation, shaping the landscape by impacting processes through trophic cascades (Smith et al. 2003). They, along with other predators, limit their primary prey's population levels through predation (Hebblewhite et al. 2002, Ripple and Beschta 2006, 2008), often selectively predating old, young, or other vulnerable individuals leading to healthier individuals within the population (Smith et al. 2004, Metz et al. 2012, Hoy et al. 2022). They also impact the spatial use of their prey through non-consumptive effects by introducing the threat of predation (Fortin et al. 2005, Mao et al. 2005, Kohl et al. 2018, 2019). These suppressed ungulate populations then impact other aspects of the landscape such as vegetation regrowth through reduced browsing (Brice et al. 2024, Hobbs et al. 2024) and healthier nesting habitat for riparian songbirds (Baril et al. 2011).

Wolves also share their space with both cougars and humans in the Greater Yellowstone Ecosystem where they all have unique impacts on an overlapping multi-prey population (Wright et al. 2006). Recreational hunting effort was used to control the population of elk that migrate beyond the boundaries of Yellowstone during the winter (Wright et al. 2006). However, with the wildlife populations within the Greater Yellowstone Ecosystem only becoming stable in recent years after the work of recolonizing predators and environmental shifts in the system (Cassidy et al. 2026), there is still a lot to learn about how these predators impact the landscape through their direct effects and interactions. In the following chapters I investigate how avian scavenger foraging is impacted by wolves in various capacities. First, I examine how the kleptoparasitism of cougar kills by wolves impacts the foraging of scavengers. Second, I investigate how wolf provided carrion impacts territorial raven foraging movements compared to carrion

created though recreational hunting outside of Yellowstone National Park. This work provides insights into how avian scavengers will respond and benefit from the continued expansion of gray wolves throughout the western US.

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Chapter 2: Interference competition by an apex predator alters avian scavenger foraging opportunities at a subordinate predator's kill

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2.1 Abstract

Interactions between apex predators can impact the strength of their trophic cascades by altering predation patterns. Studies have investigated the different ways that subordinate predators may be affected by interference competition of dominant predators, but they have only hypothesized about how scavengers may be impacted by these interactions. We investigated how four avian scavengers in Yellowstone National Park access carrion in an ecosystem with two apex predators with different foraging and competition strategies, gray wolves and cougars. We predicted that avian scavengers would be less abundant at cougar kills as cougars exert more effort concealing and defending their kills than wolves. We also predicted that wolf kleptoparasitism events at cougar kills would increase the abundance and activity of avian scavengers by making kills easier to find and less risky to visit. We monitored 32 wolf kills and 27 cougar kills between 2021 – 2025 and explored two metrics of avian scavenger use of kill sites: the maximum count at a kill site on a given day and the activity rate, which sums all the detections across a day to estimate the time spent associating with the resource. We found that scavengers responded to the competition strategies of predators as predicted, having greater maximum counts at wolf kills than cougar kills. Species varied in the strength of their response to the primary predator of the kill. Maximum counts of common ravens and bald eagles were greater at wolf kills and declined quicker over time than at cougar kills. Maximum counts of black-billed magpies and golden eagles were more similar at kills from both predators, with only counts of golden eagles decreasing faster over time at wolf kills. We found evidence that wolf kleptoparasitism events impacted scavengers at cougar kills. Ravens and bald eagles increased their activity rates on days with wolf activity at cougar kills, whereas they were not active at cougar kills in the absence of wolves. In contrast, magpies and golden eagles were active at cougar kills in the absence of wolves and saw an increase in their maximum counts on days with wolf activity that did not translate into higher activity rates. Our findings suggest that predator competition strategies mediate

scavenger foraging and that the kleptoparasitism between predators with contrasting competition strategies can improve scavengers' ability to use the subordinate predator's kills through the disruption of those competition strategies.

2.2 Introduction

Apex predators can play vital roles in maintaining the health and stability of ecosystems (Estes et al. 2011, Ripple et al. 2014) through regulation of both prey and subordinate carnivores, creating trophic cascades (Ceccarelli et al. 2006, Mäntylä et al. 2011, Hollings et al. 2014, Suraci et al. 2016, Hammerschlag et al. 2025). Studies highlighting trophic cascades often isolate the impacts of a single predator (Montgomery et al. 2019). Yet, interactions between sympatric predators can shape the nature and strength of top-down effects (Strong 1992, Sih et al. 1998, Krofel et al. 2012, White et al. 2024). For example, when killer whales (*Orcinus orca*) prey upon sea otters (*Enhydra lutris*), they can dampen their top-down effects on sea urchins and reduce the health of kelp forests (Estes et al. 2004). Alternatively, increasing the complexity of the invertebrate predator guild in marsh ecosystems lowers primary production as intra-guild predation and interference competition reduce predation on herbivores (Finke and Denno 2004, Otto et al. 2008). Understanding the complexities of specific interactions and their top-down effects can provide insight for managers looking to restore large carnivore guilds.

Research into the impacts of high-level trophic interactions has largely focused on direct predation pathways, leaving indirect pathways comparatively underexplored. Scavenging is an indirect pathway by which trophic cascades impact the health of ecosystems through the timely removal and redistribution of biomass (DeVault et al. 2003). Beyond subsidizing scavenger foraging by reducing the dependence of carrion availability on environmental conditions (Gese et al. 1996, Wilmers and Getz 2004, Pereira et al. 2014), predators mediate scavenger access to carrion through competition strategies that minimize biomass loss to kleptoparasitism. For example, the caching behavior by felids delays scavenger presence and invertebrate activity (Balme et al. 2017, Teurlings et al. 2020). Recent studies investigating high-level trophic interactions have theorized that kleptoparasitism by a dominant predator may alter the benefits conferred to other scavengers by the subordinate predator (Krofel et al. 2012, White et al. 2024), yet this

area remains untested. One potential impact is that the subordinate predator's competition strategies may be disrupted, altering the numbers and foraging opportunities of scavengers.

Gray wolves (*Canis* lupus) and cougars (*Puma* concolor) are two of North America's top predators, and both contribute to the flow of nutrients through their ecosystems by providing and regulating the availability of carrion to scavengers (Wilmers et al. 2003, Wilmers and Getz 2004, Allen et al. 2015, Elbroch et al. 2017, O'Malley et al. 2018). Both predators have evolved different behavioral strategies to minimize the loss of biomass to scavenger kleptoparasitism. Cougars are ambush predators that have high hunting success rates and the ability to take down large adult ungulates with minimal disturbance (Husseman et al. 2003, Ruth et al. 2019). Cougars attempt to prevent the loss of biomass to scavengers by dragging their kills below cover and caching them beneath snow, sticks, and dirt to reduce their detectability (Stahler et al. 2002, Allen et al. 2023). Cougars pose a high mortality risk to mesocarnivores at their kills, and their immediate presence deters smaller scavengers, such as mesocarnivores and birds (Allen et al. 2015, Ruprecht et al. 2021, Binder et al. 2026a).

Wolf competition strategies to limit scavenger kleptoparasitism stand in stark contrast to the stealth and active defense used by cougars. Wolves are easy for scavengers to detect during winter as they travel and hunt in large groups, often through open terrain, making them visually obvious on the landscape. Avian scavengers investigate wolves exhibiting hunting behavior, often arriving before the prey is brought down (Stahler et al. 2002). Eavesdropping on wolf communication also allows scavengers to locate wolves over large distances (Harrington 1978). To compensate for their lack of stealth, wolves minimize the biomass they lose to scavengers by gorging themselves and maximizing their intake before scavengers can feed (Mech 2002, Wilmers et al. 2003). They then consume the remainder of the carcass over the course of several days, providing only minimal defense against scavengers when not actively feeding. Mortality risk for avian scavengers from feeding wolves is low (Richman et al. 2025).

In this study, we leverage the intact predator guild within Yellowstone National Park, a system where several large carnivores have recolonized the landscape following decades of absence, to examine how apex carnivore interactions shape the flow of biomass to scavengers. First, we hypothesized that the contrast in the use of limiting detection and active defense of kill sites in the competition strategies of

wolves and cougars would lead to variation in scavenger use of carrion, and we predicted that abundance of avian scavengers would be lower at cougar kills. Second, a group of wolves are considered dominant to cougars and will take control of cougar kills when discovered, removing the threat of the cougar on scavengers. Wolves will also undo any caching the cougar has done, which may make it easier for scavengers to detect. Wolves will even navigate the landscape to increase their chances of these interactions (Kortello et al. 2007, Orning 2019, Rabe et al. 2025, Binder et al. 2026*b*). Thus, we further hypothesized that wolves disrupting cougar competition strategies would influence avian scavenger abundance and activity at cougar kills. We predicted that avian scavengers would respond in the same way to wolf kleptoparasitism of a cougar kill as they would to wolf kills, increasing abundance and time spent at the cougar kill. This provides insight into how sympatric top predators influence the nutrient flow to scavenger communities through behavior and competitive interactions.

2.3 Methods

2.3.1 Study area

The northern range of Yellowstone National Park is a 1530 km^2 area along the northern boundary of the park encompassing part of the Yellowstone River watershed that has a high density of predators and prey during the winter (Fig. 1). The year-round resident cougar population in the northern range was last estimated at 34-46 individuals (Cassidy et al. 2026). The northern range was also used by 4-8 wolf packs and by various dispersing individuals (Cassidy et al. 2026). Elk (*Cervus canadensis*) have been the primary prey for both cougars and wolves during the winter, although as elk populations have declined, both predators have shifted their prey base to include mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), mountain goat (*Oreamnos americanus*), bighorn sheep (*Ovis* canadensis), and bison (*Bison bison*; Metz et al. 2012, Ruth et al. 2019, Rabe et al. 2025). Winter in the northern range lasts from November to early April with average temperatures ranging from -12ºC to 13ºC (Cook 1993) and snowfall amount and timing (onset and melt) varying widely from year to year. The winter scavenger guild in Yellowstone consists of 7 primary species: wolf, coyote (*Canis latrans*), golden eagle (*Aquila* chrysaetos), bald eagle (*Haliaeetus* leucocephalus), red fox (*Vulpes*

vulpes), common raven (*Corvus corax*), and black-billed magpie (*Pica hudsonia*). In this analysis we focus on the avian scavengers due to limitations in the ability to sample wolf kills at night when mesocarnivores are active (Klauder et al. 2021, Binder et al. 2026a).

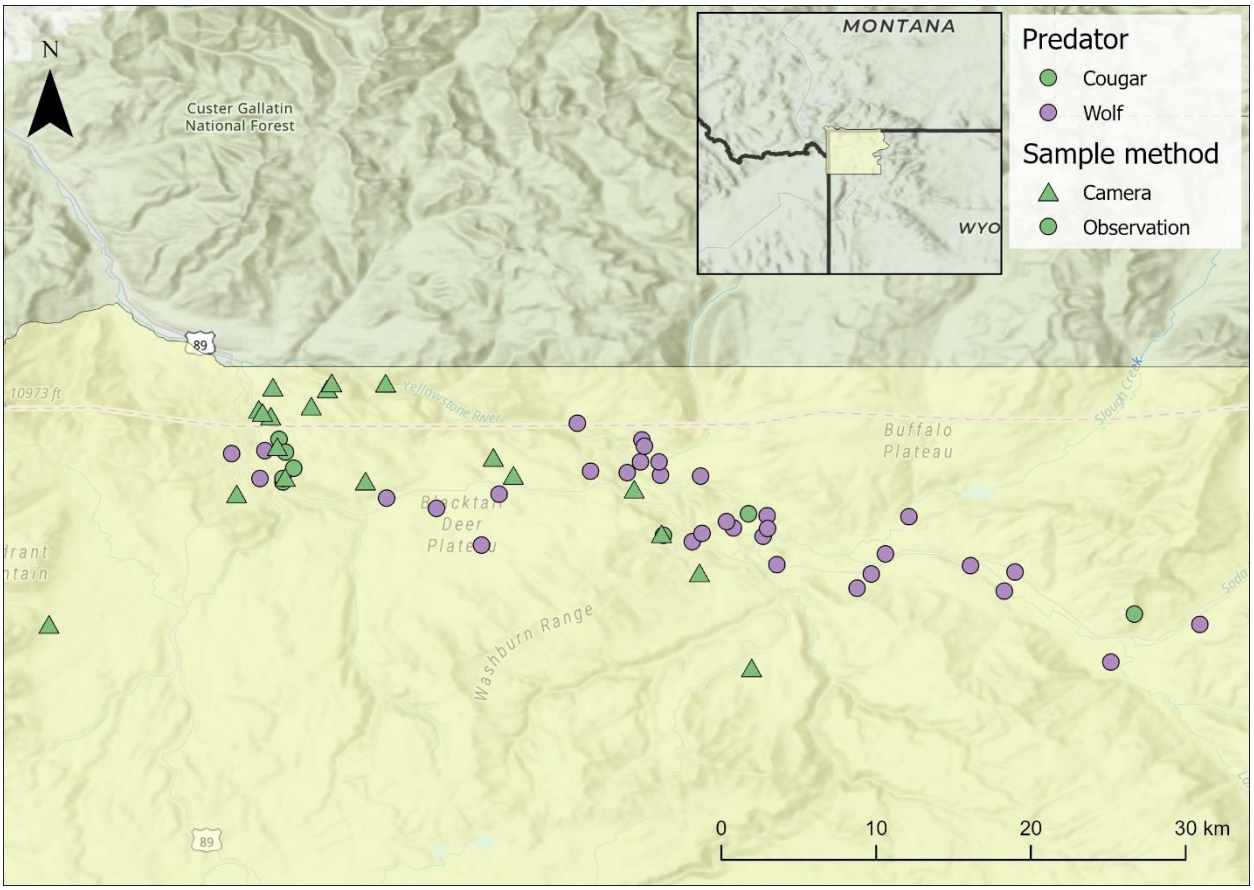

Figure 1. The locations of sampled wolf (purple) and cougar (green) kills in Yellowstone National Park. Triangles indicate cougar kills that were sampled using cameras traps (circles are direct observations).

2.3.2 Collecting scavenger count data

We gathered data on scavengers at wolf kills using the observation method employed by Wilmers et al. (2003). We utilized radio and global positioning system (GPS) collars deployed by the Yellowstone National Park's Wolf Project to detect wolf kills by tracking packs using radio telemetry and investigating clusters of GPS points likely to be kills (Anderson and Lindzey 2003, Metz et al. 2012). We then performed counts of scavengers and predators interacting with the carcass (*at the carcass*, AC), within 15 m (*carcass arena*, CA), and within 500 m (*field of view*, FOV*)* using a Vortex Razor HD 27-65x85 spotting

scope and Swarovski 10x42 EL binoculars. These areas are separated to note the number of individuals feeding (AC), competing for access (CA), and within detection range (FOV). We performed scavenger counts at 10 min intervals throughout daylight hours for up to seven days.

Similarly to wolves, cougars were captured and equipped with GPS collars by the Yellowstone National Park's Cougar Project, which were used to locate kills by visually inspecting GPS points and investigating spots likely to be kills based on grouping and movement patterns (Anderson and Lindzey 2003, Rabe et al. 2025). We programmed camera traps (Browning Spec Ops Elite HP5) to take 5 or 20 s videos with a 1 min cooldown period to capture the number of scavengers utilizing the carcass over time while minimizing the chance of prematurely ending sampling by depleting the batteries or filling the memory card. We set two cameras at kill sites at different angles to cover a wider area and allow some movement of the carcass without losing it from the viewshed. To monitor kills from individuals being monitored for other studies where camera deployment may lead to premature abandonment of the kill, we instead utilized the direct observation method used for wolves, and carcasses were observed for up to 9 days.

We limited scavenger counts from direct observation data to individuals counted within 15 m (AC and CA) of the carcass to better match the camera's view shed (Fig. 2). We processed camera data using Timelapse2 to record the minimum number of individuals present in each video as unique individuals could not be reliably identified. We then restricted the camera data to daylight hours based on sunrise times from the suncalc package (version 0.5.1; Thieurmel and Elmarhraoui 2022).

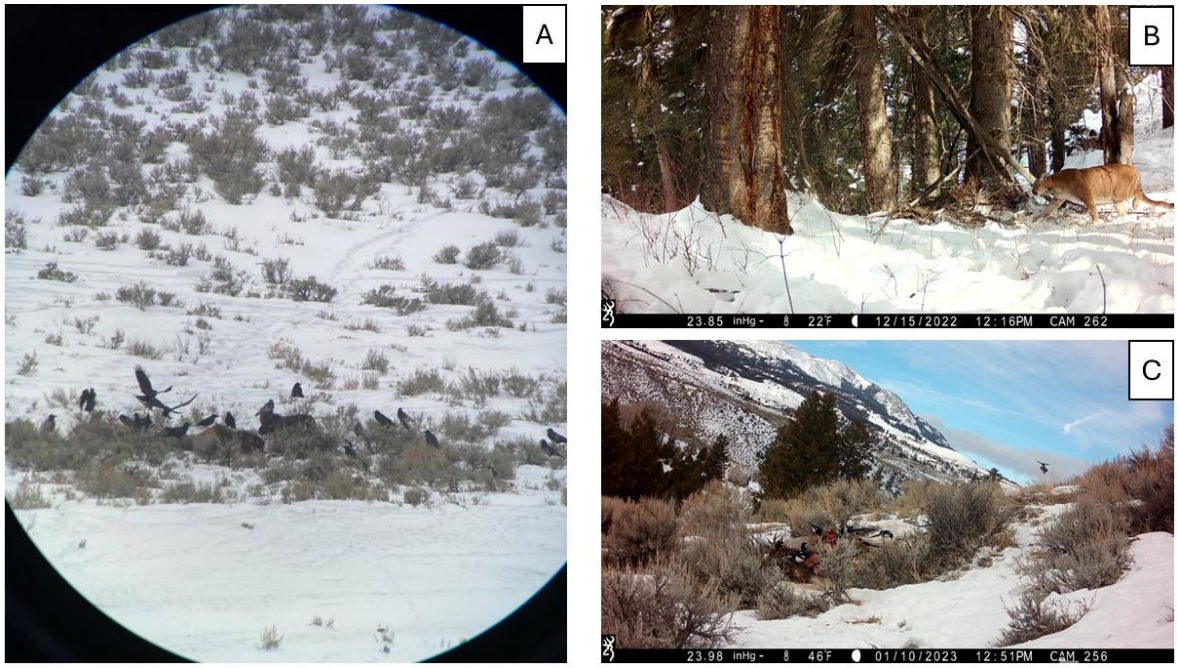

Figure 2. Example images showing a typical viewshed for kills monitored using direct observation (A) and camera trapping (B, C).

2.3.3 Quantifying scavenger use of carrion

We quantified scavenger usage of carcasses using two different metrics that represent different aspects of scavenger foraging that may change: (1) the daily maximum count and (2) activity rate. The maximum count provides the best estimate of the number of individuals that are utilizing the carcass as individuals were not identifiable. Activity rate allows the recounting of individuals, incorporating an aspect of time, to determine how long a species was associated with the carcass each day. We defined maximum count as the maximum number of individuals detected simultaneously each day. We defined the activity rate as the total number of detections divided by the amount of time observed. To calculate the activity rate, we first restructured the camera data to match the observation data by applying an artificial 10 min sampling schedule starting each day at the time of camera deployment or at sunrise, and ending at sunset. At each 10 min interval, we kept the greatest count of each species from videos taken up to 2 min after the 10 min marker. An intervals count was 0 when no videos were taken within that 2 min period. We then calculated the activity rate by summing the counts from all the intervals and dividing by the number of sample

intervals. We calculated the activity rate before and after a wolf was detected each day, with the entire day being considered “before wolves” when no wolves were detected.

2.3.4 Wolf presence at cougar kills

We defined wolf kleptoparasitism as a binary variable that indicates whether a wolf was detected at a cougar kill each day. Unlike the scavenger direct observations that were restricted to the *carcass arena*, we considered the full *FOV* for wolf detection to ensure that all instances of wolves at the carcass were captured. All occasions where wolves were detected within the *FOV* led to their discovery of the cougar kill during visual observations, even if their direct presence at the carcass was not captured due to the 10 min sampling periods.

2.3.5 Kill site covariates

We considered two landscape variables around kill sites, tree cover and roughness, as factors that may impact kleptoparasitism by limiting the ability of scavengers to detect predator kill sites by obstructing lines of sight. We obtained tree cover estimates in the northern range from the Rangeland Analysis Platform on a 30x30 m scale (Allred et al. 2021). We selected this smaller cell size as it is likely to better represent the visual obstruction to avian scavengers whereas a larger cell size starts incorporating more habitat preference.

Roughness measures the average difference in elevation between a cell and its neighbors, and values on a 30x30 m scale were acquired from previous work (Kohl et al. 2019, Ruth et al. 2019, Rabe et al. 2025). We defined a kill site’s roughness as the average value of the cells within 250 m of the kill site to described terrain roughness and capture different habitat that could affect the detection of the carcass.

Another factor that likely affects the number of scavengers is the prey size. Large prey are easier to detect (Rabe et al. 2025) and offer scavengers more biomass. Information about prey species, age, and sex was recorded by using visual cues from a distance (e.g. antlered elk indicating adult male elk) or by kill site investigations done as part of the Yellowstone Wolf, Cougar, and Elk winter predation study to record demographic information, health condition, and cause of death of the prey (Metz et al. 2012). We obtained estimates of edible prey biomass by using species, age class (calf, yearling, adult), and sex

specific weight estimates for elk, deer (Murphy et al. 1998), bison (unpublished data Yellowstone Bison Office), coyotes (Crabtree and Sheldon 1999), mountain goats (Festa-Bianchet and Côté 2023), bighorn sheep (Krausman and Bowyer 2023), and badgers (*Taxidae taxus*; Lindzey 1971). Elk, deer, and bison biomass estimates were calculated from a growth curve during the early (November and December) and late (March) winter (Murphy et al. 1998). For elk, deer, and bison killed in midwinter months (January and February), an average of late and early winter edible biomass was used. In the absence of sufficient evidence to determine the age or sex of a prey item, an average of the relevant categories was used (e.g., unknown sex is an average of male and female weights).

We also considered the number of days since the predation event to account for the reduction in the amount of biomass available as it is consumed, as well as probability of detecting a kill increasing over time. We expected both conditions to differ by predator as a group of wolves can consume biomass more quickly, and cougar caching makes it more difficult to immediately locate the kill.

2.3.6 Modeling scavenger communities at cougar and wolf kills

We investigated the usage of cougar and wolf kills by avian scavengers by examining the impact of the primary predator on the maximum count of each scavenger species. We fit species-specific generalized linear mixed models (GLMM) in R (version 4.5.1; R Core Team 2025) using the package glmmTMB (version 1.1.14; Brooks et al. 2017). We evaluated potential overdispersion in maximum observed count using the performance package (version 0.16.0; Lüdecke et al. 2021) to examine the observed variance in the model fit with the Poisson, refitting with a Negative Binomial when overdispersion was detected. The maximum observed count for each species on day *i* at kill site *k* followed a Poisson or negative binomial distribution, such that:

$$\mathrm{Count}_{ik} \sim \mathrm{Poisson}(\lambda_{ik}) \text{ or } \mathrm{NegBin}(\lambda_{ik}, \theta)$$

$$lg(\lambda_{ik}) = \gamma_{0k} + \gamma_1 * Wolf_k + \gamma_2 * Day_{ik} + \gamma_3 * Tree_k + \gamma_4 * Roughness_k + \gamma_5 * Biomass_k + \gamma_6 * (Wolf_k * Day_{ik})$$

where γ_{0k} is a random intercept for kill site as kills were often observed for multiple days. Data were restricted to the first seven days after the kill as that was the longest duration a wolf kill was directly sampled.

2.3.7 Modeling impact of wolf kleptoparasitism at cougar kills

We assessed if wolf kleptoparasitism of cougar kills affected two metrics of scavenger foraging: maximum count and activity rate. We modeled both metrics using species-specific Poisson or negative binomial GLMMs. We evaluated potential overdispersion in maximum observed count and activity rates using the performance package (version 0.16.0; Lüdecke et al. 2021) to examine the observed variance in the model fit with the Poisson, refitting with a Negative Binomial when overdispersion was detected. Data were restricted to the first nine days after the kill as that was the longest duration a cougar kill was sampled through observation. The maximum count of each species on day *i* at kill site *k* followed a Poisson or negative binomial distribution based on the overdispersion, such that:

$$Count_{ik} \sim Poisson(\lambda_{ik}) \; or \; NegBin(\lambda_{ik}, \theta)$$

$$log(\lambda_{ik}) = \alpha_{0k} + \alpha_1 * Visit_k + \alpha_2 * Day_k + \alpha_3 * Method_k + \alpha_4 * Tree_k + \alpha_5 * Roughness_k + \alpha_6 * Biomass_k$$

where α_{0k} represents a random intercept for kill site. Activity across a 10-hour period on day *i* at kill site *k* also followed a Poisson or negative binomial distribution, such that:

$$ActivityRate_{ik} \sim Poisson(\lambda_{ik}) \; or \; NegBin(\lambda_{ik}, \theta)$$

$$log(\lambda_{ik}) = log\,(duration/60) + \beta_{0k} + \beta_1 * Visit_k + \beta_2 * Day_k + \beta_3 * Method_k + \beta_4 * Tree_k + \beta_5 * Roughness_k + \beta_6 * Biomass_k$$

where β_{0k} representing a random intercept for kill site and log(duration/60) is an offset to account for the number of daylight observations that could be taken for each day i due to changing day length throughout the winter. We considered a covariate to be statistically significant at $p \leq 0.05$ and discuss covariates at $p \leq 0.1$ as having weak evidence of an effect.

Table 1. Data types and descriptions for covariates used in the maximum count and activity rate models for common raven, black-billed magpie, bald eagle, and golden eagle.

Covariate	Type	Description
Wolf	Binary	1 indicates if the kill was from wolves and 0 for cougar kills, otherwise 0
Visit	Binary	1 indicates if a wolf was detected at a cougar kill during daylight hours on each day, otherwise 0
Day	Continuous	Number of days since the predation event occurred
Method	Category	1 indicates if the sample method was direct observation; 0 if it was camera trapping
Tree	Continuous	Percent tree cover of the 30x30 m cell the kill site is located within
Roughness	Continuous	Average terrain roughness of the 30x30 m cells in a 200 m radius around the kill site
Biomass	Continuous	Estimated biomass of the prey (see text for details)
Duration	Discrete	The number of 10 min sampling periods during each day. This is either the number of daylight observations or the number of observations before and after wolves are detected

2.4 Results

We gathered observations from 59 kills (n_{cougar} = 27, n_{wolf} = 32) during the winter months of 2022 - 2025 (November – March, Fig. 1). Of those, 40 were directly observed and 19 were cougar kills monitored with cameras. Wolf kill sampling was initiated a mean of 0.63 days (range = 0 - 5, sd = 1.2) after the predation event as hunting sequences were often seen. Cougar kill sampling started later at 1.6 days (range = 1- 4, sd = 0.83) after the predation event because detection was delayed by GPS upload schedules. For kills observed through direct observation, sampling duration lasted a mean of 2.5 days after a wolf kill (range = 0 – 7, sd = 2) and a mean of 4.9 days after a cougar kill (range = 2 – 9, sd = 2.5).

We detected both ravens and magpies at 96.9% of wolf kills while we detected golden eagles at the fewest (59.4%, Table 2). We detected magpies at cougar kills the most (92.6%) and bald eagles were detected the least (14.8%, Table 2). Coyotes and red foxes often scavenged at kill sites as did other species, like pine marten and mountain chickadees, that were detected less frequently (Appendix A: Table S1). Detections continued to occur at cougar kills sampled using cameras after the nine-day period considered for modeling; however, behavior during these events was often investigative (e.g. digging, sniffing) as biomass remaining was minimal. Wolves were detected at least once during daylight at 37%

of cougar kills (10) and on 13 separate days. Cougars returned to kills visited by wolves six times, although most of these incidents were at night (4), and the other instances were at dusk (2).

Table 2. The median maximum count (and range) and the percentage of kills where each avian scavenger species was detected on at least one day during the nine days after the predation event (n_{wolf} = 32, n_{cougar} = 27). Values for wolf kills were restricted to within 15 m of the carcass.

	Wolf		Cougar	
	Presence	Median count	Presence	Median count
Raven	96.9% (31)	32 (0 – 75)	63% (17)	1 (0 – 40)
Magpie	96.9% (31)	12 (0 – 23)	92.6% (25)	8 (0 – 26)
Bald eagle	71.9% (23)	1 (0 – 11)	14.8% (4)	0 (0 – 3)
Golden eagle	59.4% (19)	1 (0 – 4)	48.1% (13)	0 (0 – 7)

2.4.1 Scavenger communities at wolf and cougar kills

Negative binomial distributions were used for the raven and magpie maximum counts, while Poisson distributions were used for the golden and bald eagle maximum counts. The maximum counts of all avian scavengers except for magpies were affected by the interaction between the primary predator and the number of days since the predation event (Fig. 3, Appendix B: Table S1). Ravens and bald eagles showed similar response patterns to the primary predator with wolf kills having a high starting value that quickly declined over time (Fig. 4). Conversely, both species had essentially no presence at cougar kills, which did not change over time (Fig. 4). Golden eagle maximum counts at wolf and cougar kills were similar in the first few days after the predation event, but counts at wolf kills declined quicker over time, similar to ravens and bald eagles (Fig. 4). Magpie maximum counts were similar at both wolf and cougar kills ($p > 0.93$, Fig. 3), both around 5 individuals on the day of the predation event (day 0) with no evidence that count declined within the sampling period ($p > 0.17$, Fig. 3, 4).

Tree cover was a significant predictor for maximum counts of magpies, with lower counts in areas with denser tree cover (Fig. 3, Appendix B: Table S1). Prey biomass had a significant positive relationship with the maximum count of all species, although golden eagles only showed weak evidence for this effect (Fig.

3, Appendix B: Table S1). Roughness at the kill site was not a significant predictor for any species ($p > 0.17$, Fig. 3, Appendix B: Table S1).

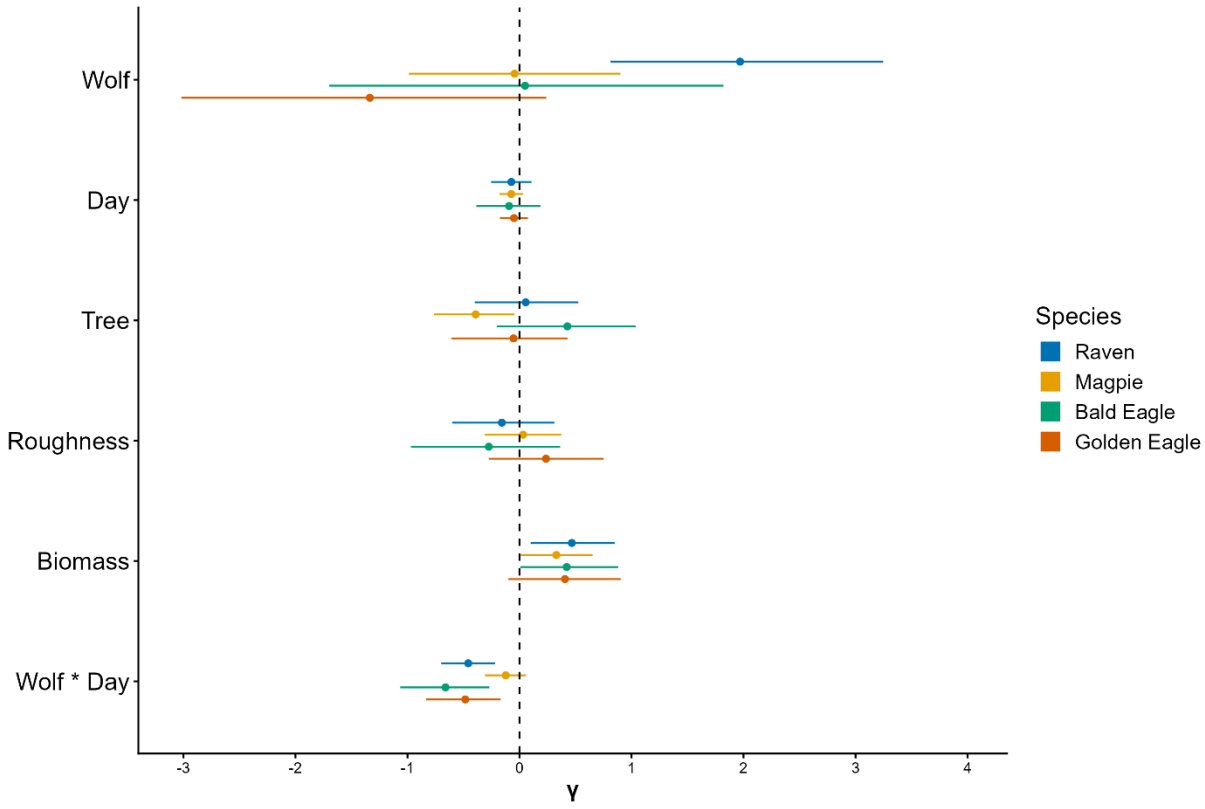

Figure 3. Mean model parameter estimates and 95% confidence intervals on the log scale for each species-specific generalized linear mixed model investigating the maximum count of avian scavengers visiting wolf and cougar kills (n_{days} = 242). We considered coefficients where the 95% CI did not cross 0 to have a significant effect. Wolf indicates if a kill site belonged to a wolf, and day indicates the number of days since the predation event.

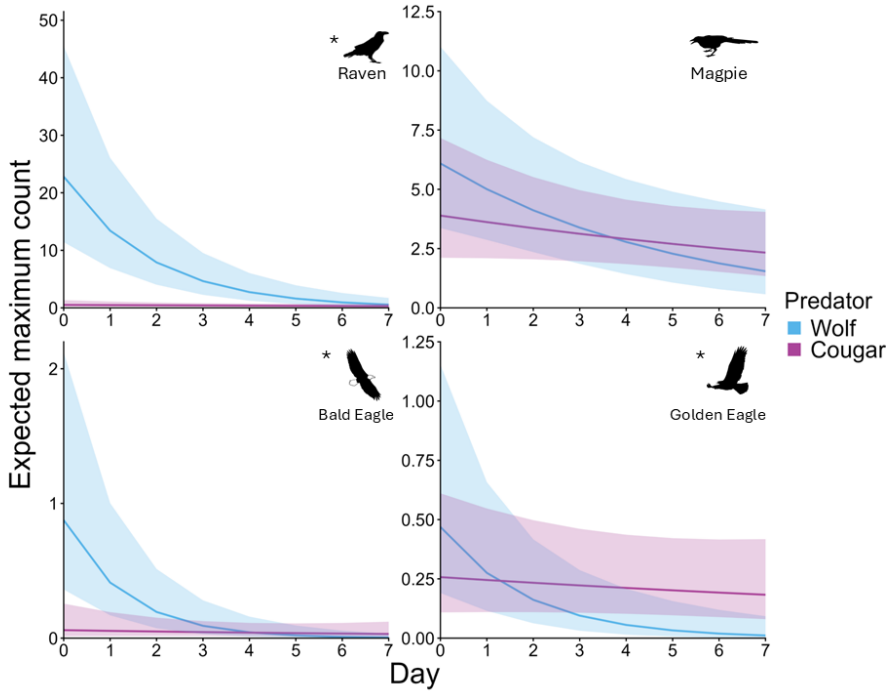

Figure 4. Expected maximum counts and 95% confidence intervals at wolf kills (blue) and cougar kills (pink) across the first week after the predation event. All other covariates are held at their mean value. An asterisk (*) indicates that the interaction effect between predator and days was significant in the model.

2.4.2 Impacts of wolf kleptoparasitism on scavenger counts

We selected the negative binomial distribution for raven and magpie maximum counts, and Poisson distributions for golden and bald eagle maximum counts. The negative binomial distribution was used for all species-specific models investigating activity rates. Wolf kleptoparasitism events at cougar kills generally had positive effects on avian scavenger maximum counts and activity rates, although species varied in which metrics were affected (Fig. 5, Appendix B: Table S2, S3). The maximum count and activity rate of ravens increased with wolf visits to cougar kills (Fig. 6, 7). Bald eagles showed weak evidence for an increased activity rate at cougar kills associated with wolf kleptoparasitism events (Fig. 7). Magpies and golden eagles shared a similar response to wolf kleptoparasitism events, with maximum counts increasing on days with a wolf activity (Fig. 6), but with no change in activity rates (Fig. 7).

Other covariates were also found to affect scavengers at cougar kills. Magpie and golden eagle maximum counts and activity rates both declined over time (Fig. 5, Appendix B: Table S2, S3). Tree cover showed

variable effects with kills near denser tree cover having lower magpie maximum counts and weak evidence for greater raven counts (Fig. 5A, Appendix B: Table S2). Prey biomass positively impacted both magpies and golden eagle maximum counts and activity rates (Fig. 5, Appendix B: Table S2, S3). The sample method only affected the ability to detect ravens, with maximum counts and activity rates both being greater for kills monitored through direct observation instead of camera trapping (Fig. 5, Appendix B: Table S2, S3). No species showed a response of either maximum count or activity rate to the roughness of cougar kill sites ($p > 0.27$, Fig. 7).

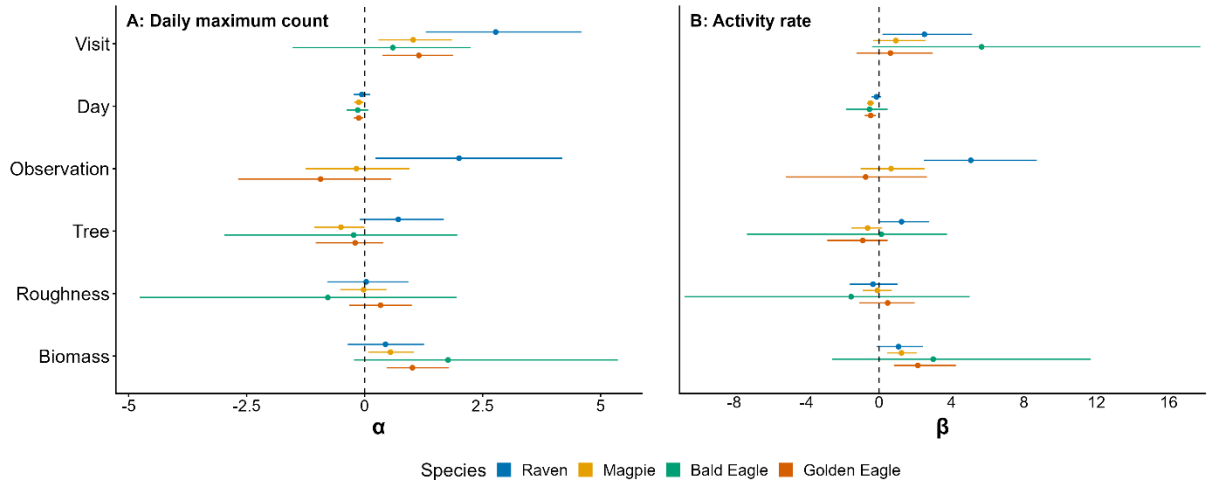

Figure 5. Mean model parameter estimates and 95% confidence intervals on the log scale for each species-specific generalized linear mixed models investigating how wolf kleptoparasitism events at cougar kills affect avian scavenger maximum counts (A, $n_{days} = 190$) and activity rates (B, $n_{days} = 201$). The result for the *Observation* covariate for bald eagles was excluded from this plot as it was not significant and reduced clarity of the full figure due to its large error. We considered coefficients where the 95% CI did not cross 0 to have a significant effect. Visit indicates a wolf being detected at a cougar kill site.

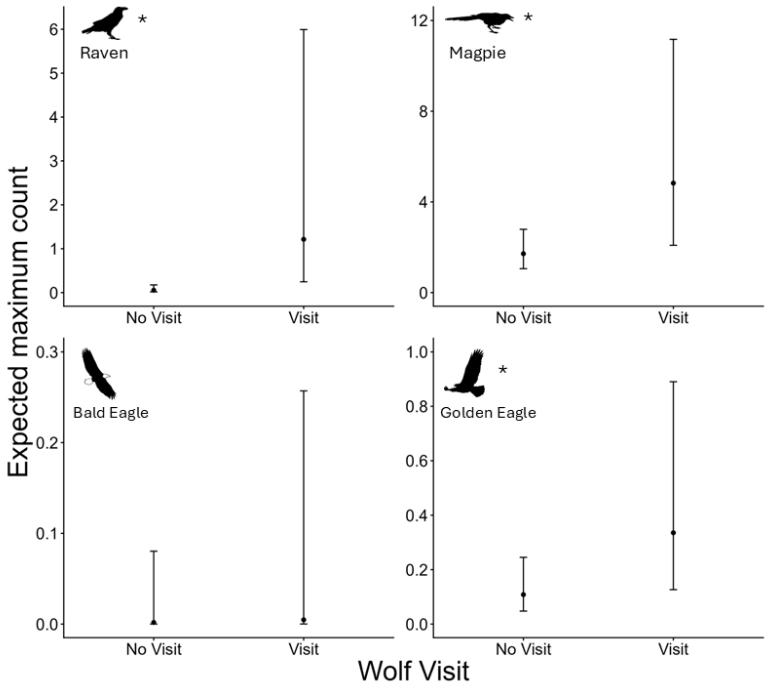

Figure 6. Expected mean maximum counts and 95% confidence intervals when wolves visit or do not visit a cougar kill site 4 days after the cougar predation event. Estimates were calculated from a simplified model, only including *Visit* and other significant covariates. All other covariates were held at 0. An asterisk (*) indicates that the visit covariate was significant in the model.

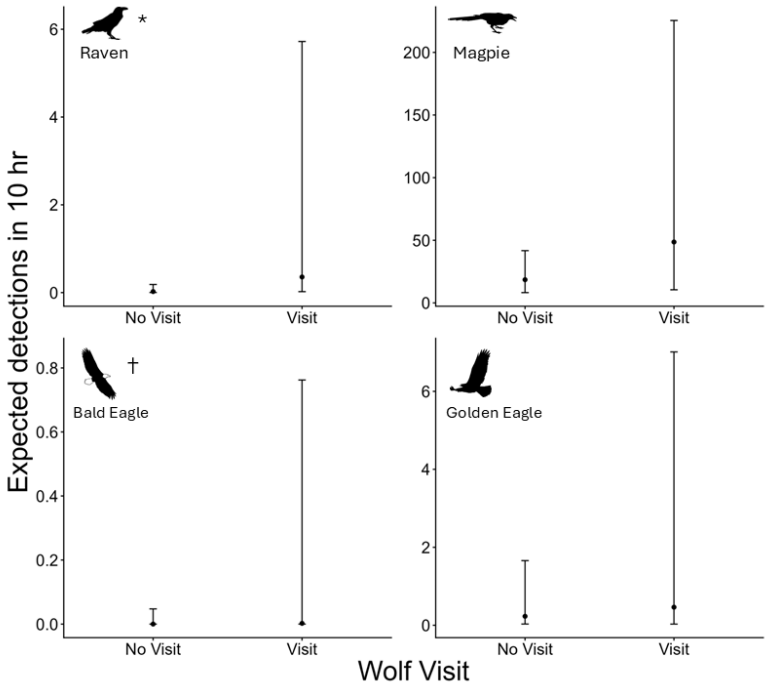

Figure 7. Expected number of detections across a 10-hour period and 95% confidence intervals when wolves visit or do not visit a cougar kill site 4 days after the cougar predation event. Estimates were calculated from a simplified model, only including *Visit* and other significant covariates. All other covariates are held at 0. An asterisk (*) indicates that the *Visit* covariate was significant in the model. A cross (†) indicates that *Visit* covariate had weak evidence for an effect in the model.

2.5 Discussion

We found a dominant predator (wolves) can create foraging opportunities for scavengers, not only through direct pathways, but also by disrupting the anti-scavenger competition strategies of a subordinate predator (cougars) through interference competition. It is important to maintain or restore all apex predator populations in a system as the carrion created by each predator may be used by a different subset of the scavenger guild. Even a single species may subsidies scavengers in a wide variety of ways throughout their range. For example, cougars in Patagonia are estimated to provide more food to scavengers than wolves in Yellowstone (Elbroch et al. 2012). Yet we find here that the carrion created by a sympatric population of the same species, cougars, has less use by avian scavengers during the winter. Foraging opportunities created by multiple predators and the interactions between them may become more important to scavengers as a warming climate can reduce the environmental stress experienced by

ungulates and lower mortality rates, especially during winter months (Wilmers and Getz 2005, Wilmers and Post 2006).

We found greater numbers of avian scavengers at wolf kills compared to cougar kills, indicating a potentially greater impact on scavenger communities. This was consistent with our predications as cougars hide their carcasses, which can then take longer to detect, and when located, access is then tempered when the cougar is present (Allen et al. 2015). All species except magpies showed a faster decline in counts at wolf kills than at cougar kills. This decline is likely driven by the foraging efficiency of wolves, which reduces available biomass to scavengers. A pack of wolves consume their kills quicker than a single cougar or even a female with kittens (Cunningham et al. 2025). Our results also indicated that edible biomass based on prey size showed a similar trend of kills, with smaller prey species having lower scavenger counts. We interpret these results to mean that scavenger presence at wolf kills is largely driven by foraging efficiency, and scavenger counts decrease quickly as the resource is consumed. Scavenger counts at cougar kills are driven more by ability to detect the carcass and access. Hidden carcasses take longer to detect, and when located, access is tempered when the cougar is present (Allen et al. 2015).

Our hypothesis of wolf kleptoparasitism events affecting scavenger presence at cougar kills was supported, although species specific responses to changes in counts and activity at cougar kills fell into two distinct categories: species with and without the propensity to use cougar kills. Ravens and bald eagles infrequently used cougar kills. Both species are wide ranging, foraging generalists that can locate other resources, including wolf kills and anthropogenic subsidies, that do not have the same limiting factors as a cougar kill (Ho et al. 2023, Wilmers et al 2003a). Wolf visits to cougar kills led to greater raven counts and greater activity for both species. This shift in behavior is driven by the imbalance in the two predators' competitive strategies. Wolves facilitate scavenger access to cougar kills either by increasing the detectability of carcass or by indicating the absence of the cougar mortality threat. Ravens and bald eagles showed the strongest responses to wolf kills when compared to cougar kills. Ravens are a prime example of a species that are neophobic of new food sources (Heinrich et al. 1995) and slower to detect new carrion sources without wolf activity (Stahler et al. 2002). Wolves alleviate both constraints by

exposing concealed kills and presenting a low mortality risk (Richman et al. 2025). In this instance, the dominant predator provides scavengers with greater access to the carcass than the subordinate predator. This is not the relationship that all dominant-subordinate predators have. Our study focused on winter, when black bears, another species dominant to cougars, are hibernating. Black bears have been shown to more strongly limit carrion availability to scavengers than cougars in California (Allen et al. 2015), thus we would expect reduced counts and activity at a cougar kill site kleptoparasitized by a black bear.

In contrast, magpies and golden eagles had non-zero baseline presence at cougar kills in the absence of wolves. This is corroborated by the primary predator models where predicted counts were similar between wolf and cougar kills. Magpies are subordinate scavengers and can be excluded from feeding at wolf kills by large groups of ravens that take up space around a carcass. Magpies will opportunistically feed when smaller groups of dominant species like wolves, coyotes, or golden eagles displace ravens, creating space, or when biomass has diminished so that other scavengers have abandoned the carcass (McKinstry and Knight 1993). At cougar kills, the exclusion comes from the cougar, resulting in a similar pattern by magpies at wolf kills. Despite magpie and golden eagle counts increasing at cougar kills on days with wolf activity, there was no corresponding increase in activity. Instead, activity at cougar kills was predominantly influenced by prey biomass and the number of days since the kill, indicating that the benefit derived by these species are constrained by biomass availability more than detection or safety. Magpies are less risk averse given their subordinate status, making the threat of mortality less discouraging when considering a potential foraging opportunity (Halley 2001). Magpies are also more agile than larger scavengers, which can lessen their risk of mortality by allowing them to more quickly take off and avoid conflicts. However, they are still limited by their ability to detect kills which is supported by having lower counts at kill sites with denser tree cover. While all four avian scavengers have the physical structures to utilize olfaction (Buitron and Nuechterlein 1985, Harriman and Berger 1986, Potier 2020), a magpie’s propensity to travel closer to the ground than other species places them in a better position to utilize olfaction to locate visually obstructed carrion. Similar reasoning to explain golden eagle use of cougar kills is not apparent.

The increase in activity for ravens and bald eagles likely translates into a greater amount of biomass acquired for these species as they would otherwise not associate with the cougar kill. Further considering that wolves navigate the landscape in a way that increases their chances of locating cougar kills (Binder et al. 2026*b*), ravens and bald eagles that frequent high cougar density areas may encounter this scenario relatively frequently leading to a greater total benefit from cougar kills than we would expect if wolves were not on the landscape. This may have implications for the daily survival and the nesting success of individuals that frequently use high cougar density areas. Given that wolves consume a substantial amount of biomass at a carcass, the amount of food remaining for individuals already using a cougar kills should be reduced. Thus, we hypothesize that magpies and golden eagles will likely derive less overall biomass from cougar kills visited by wolves. However, we were unable to quantify the full implications of wolf kleptoparasitism of cougar kills on the amount of biomass acquired by individual scavenger species due to our small sample size and our data only sampling scavenger activity in short bursts throughout the day.

Previous work has been done by Wilmers et al. (2003a) to estimate active consumption rates of scavengers at wolf kills. However, future studies interested in quantifying specific changes to scavenger biomass acquisition at cougar kills should consider the unique challenges posed by cougar competition and foraging behaviors. Cougars initially feed out of the body cavity so that much of the exterior remains intact, limiting foraging space as birds cannot penetrate thick hide. Cougars also cache kills, which reduces initial detection, but also creates an additional physical barrier to avian scavengers. Together, these factors create spatially constrained feeding conditions in which intensified competition among individuals should suppress individual feeding rates. Wolf kleptoparasitism may change these factors as they will tear apart animal hides during their foraging and dig carcasses out of caches, increasing access for scavengers (Selva et al. 2003).

Wolves as kleptoparasites have broader negative effects on cougars, reducing the biomass cougars acquired from their own kills and shortening their kill intervals after being displaced (Rabe et al. 2025). Despite our findings that wolves increasing the numbers and activity of avian scavengers at cougar kills, we believe that this additional scavenger activity does not play an additive role in changing cougar

predation patterns. Any additional biomass taken by avian scavengers associated with wolves will often be beyond the cougar's biomass threshold for abandonment. We recorded cougars returning to kills that wolves had fed on, although they quickly abandoned the sites, likely because little biomass remained. For subordinate predators with high hunting success like cougars, remaining at kills usurped by dominant predators may be inefficient relative to their agency to hunt. This stands in contrast to wolves, who are inefficient hunters, that showed decreased kill intervals as a result of grizzly bear interference competition as they would not abandon kills monopolized by grizzly bears (Tallian et al. 2017). The increase in biomass acquired by avian scavengers associated with wolf kleptoparasitism of cougar kills is more consequential at the individual scavenger level, potentially benefiting their survival or breeding success.

An unexpected result from our study was the positive response of ravens to tree cover. Magpies responded as expected, with counts declining at cougar kills in areas of greater tree cover, consistent with the expectation that dense vegetation impedes visual detection. One potential explanation for the observed raven response is that trees provide safe perching locations that ravens can observe carcasses from that are beyond the reach of the cougar. In areas with no tree cover, stopping at a site requires landing on low vegetation or open ground. Cougars present a real mortality risk to scavengers (Allen et al. 2015, Ruprecht et al. 2021), and we observed multiple occasions of cougars returning to kills immediately after walking away to bed or abandoning them (>100 m) when a magpie landed around the carcass.

A shared landscape with multiple predators can lead to increased benefits for scavengers. More predator species not only add additional hunting individuals, but scavenger species are able to derive different amounts of benefit depending on the predator's competition strategy and the life history of the scavenger species. When sympatric predators have mismatches in their nutrient flow to scavengers due to varying competition strategies, intra-guild interactions such as interference competition can make species associate with the subordinate predators kills in ways that contradict how an investigation of a single predator would predict. Avian scavengers take advantage of this, and it is likely that mesocarnivores that frequently utilize predator carrion may see similar effects, although we were unable to investigate this hypothesis. How this energy pathway may provide further support for certain members of the scavenger guild should be considered when considering the recovery of multi-predator landscapes.

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Chapter 3: Common raven (*Corvus corax*) winter movement driven by availability of anthropogenic and natural carrion

This work was coauthored by John Marzluff, Beth Gardner, Wesley Binder, Daniel Stahler, and Matthias-Claudio Loretto. At the time of publication of this thesis, it was not in review at a journal.

3.1 Abstract

Optimal foraging is used to predict the decisions of individuals in relation to their resources. Common ravens (*Corvus corax*) present a compelling case study for investigating whether movement decisions of place-bound scavengers follow predictions of optimal foraging theory and are informed by the availability and spatial patterns of carrion. In Yellowstone National Park, territorial ravens often travel away from their territories during the day to forage in distant areas, returning to their territories in the evening to roost. In this study, we investigate how this commuting behavior is influenced by the availability of two carrion sources: carrion used by wolves and recreational human hunting. We tracked the daily movement decisions of 18 territorial ravens (12 F, 6 M) using GPS data loggers and modeled their commuting as two separate decisions with Bernoulli generalized linear mixed models: whether to leave the territory, and if they did leave the territory, whether to visit recreational hunting areas. We found that ravens left their territories less often on days which they were recorded visiting a wolf kill within their territories, whereas available wolf kills without a documented visit did not affect departures. After leaving their territories, we found that a raven's decision to visit the hunting area was more complex. Ravens were less likely to visit the hunting areas if they visited a wolf kill outside their territory and were more likely to visit the hunting areas during periods with active hunting; although, we found no evidence that ravens were responding to changes in the predicted amount of biomass available. Ravens also visited the hunting regions less often when their territories were far away, increasing travel costs. Both the decision to leave the territory and visit the hunting area were impacted by daily snow depth and the movement decisions of other territorial ravens. Overall, we found that the commuting decision of territorial ravens does align with predictions from optimal foraging theory and that ravens are responding according to their knowledge of the timing and location of available carrion.

3.2 Introduction

Optimal foraging theory attempts to capture the decision-making process individuals undergo when trying to maximize energy intake, including which patches to forage in and when to leave those patches (Pyke 1984). To maximize fitness, individuals should forage in patches where calorie intake is greatest and move to a new patch when the foraging efficiency of that patch exceeds that of the original patch (MacArthur and Pianka 1966, Pyke 2019). However, because omniscience about distant patches is often unattainable, this decision may not be precise, as comparisons between foraging patches cannot be made accurately (Klaassen et al. 2006). Individuals must leverage knowledge of local patterns to make calculated risks about foraging (Pyke 1978, 1984). Ultimately, this decision becomes more challenging to optimize as patches become less predictable.

Scavengers rely on inherently unpredictable, ephemeral resources. Carrion availability varies with prey distribution, population size, and the hunting success of local predators (Husseman et al. 2003, Bump et al. 2009, Cristescu et al. 2022, Bartel et al. 2024). The availability of carrion also varies spatially and temporally from year to year due to weather conditions, leading to animal deaths from starvation or exposure (Houston 1982, Gese et al. 1996). In response to this variability, scavengers have evolved efficient movement patterns and heightened senses to locate carrion (Ruxton and Houston 2004, Naves-Alegre et al. 2022). However, when deciding among multiple sources of possible carrion, optimally foraging scavengers must weigh the costs of travel against the probability of finding food.

Anthropogenic and natural resources present scavengers with differing spatial and temporal predictability (Wilmers et al. 2003*b*). Foods provided by people can be more predictable in space and time than those created by predators (Bartumeus et al. 2010, Cortés-Avizanda et al. 2012). For example, human hunters often “field dress” large, harvested animals, leaving behind edible biomass in gut piles containing organs, bones, and hide that can be more predictable in space and time than those created by predation (Wilmers et al. 2003*b*). In gray wolf (*Canis lupus*) dominated systems, natural carrion is temporally unpredictable due to wolves’ low hunting success rate (MacNulty 2002) and occurs across a wide spatial scale (Wilmers et al. 2003*b*). While this difference in carrion predictability does not always result in variation in overall

usage by scavenger population (De Pelsmaeker et al. 2024), it can impact the decision making of individuals (Loretto et al. 2026).

Common ravens (*Corvus* corax) are foraging generalists and facultative scavengers with a high movement potential due to efficient gliding flight (von Axel *in prep*). They evolved during the Pleistocene with wolves and humans and use carrion from both species (Marzluff and Angell 2005, Kearns et al. 2018). Ravens have learned to associate the presence of wolves and their communication (Harrington 1978, Stahler et al. 2002), as well as the sight and sounds of human hunters (White 2005, Marzluff et al. 2021), with potential foraging opportunities. Ravens adjust their space use depending on human and wolf provisioning, utilizing wolf-habitat more than anthropogenic landscapes in winters with higher wolf prey-acquisition rates (Walker et al. 2018). Territory-holding ravens defend areas around their nesting and roosting sites year-round (Heinrich 1988); however, they are not as restricted in their use of space when free from parental duties outside of the breeding season (Ho et al. 2023). This gives them the opportunity to decide how to optimize their time to use these various resources.

To better understand how variation in the availability of carrion from natural and anthropogenic sources influences the movement decisions of territory-holding ravens, we monitored their movements in Yellowstone National Park. Wolves were reintroduced to the landscape in 1995 and have since returned to a healthy, stable population level (Cassidy et al. 2025). Their return to the landscape contributed to more consistent provisioning of natural carrion throughout the year (Wilmers et al. 2003*a*, Wilmers and Getz 2004). Yellowstone is surrounded by private and public lands that permit recreational ungulate hunting during the winter. These two carrion sources are both readily used by common ravens, and ravens that hold breeding territories within Yellowstone National Park commute during the winter between their territories and hunting areas outside the park boundaries (Wilmers et al. 2003*b,* Marzluff et al. 2021, Ho et al. 2023).

We investigated two movement decisions made by territorial ravens during the non-breeding season: 1) when to leave the territory, and 2) where to travel after leaving the territory. We hypothesize that movement decisions will be compatible with optimal foraging theory. Yellowstone is a large park and thus, traveling to areas outside of the park for foraging opportunities carries time and effort costs. To maximize

energy benefits while minimizing costs, we predicted that ravens would be less likely to leave their territories when there is a wolf kill within their territory, providing a proximate food resource. We also expected that ravens would be less likely to leave when less recreational hunting biomass was available, making a commute an inefficient use of time and effort. After a raven leaves its territory, we predicted it would visit recreational hunting regions more often when hunting biomass availability was greater, and no wolf kill is encountered while traveling to provide a more immediate foraging opportunity.

3.3 Methods

3.3.1 Study area

Yellowstone National Park is a large (8903 km^2), mostly intact temperate ecosystem with sagebrush steppe, montane grasslands, mixed conifer and deciduous forest, and thermally active regions. Inside the park, a relatively dense wolf population creates carrion. In contrast, high levels of recreational hunting occur outside the northern boundary of Yellowstone in a mix of public and private land. Hunters target elk (*Cervus canadensis*) and bison (*Bison bison*) that migrate from Yellowstone during the winter and resident populations of mule (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) when winter conditions drive ungulates to lower elevations (Geremia et al. 2011, Rickbeil et al. 2019).

We defined two areas corresponding to the Montana Fish, Wildlife, and Parks (MTFWP) rifle hunting season and the tribal bison hunting season. During the MTFWP rifle hunting season, elk and deer are the target species. We delineated a region recreational hunters use as elk migrate out of Yellowstone (Fig. 8) by buffering (5 km, a reasonable hunter travel distance) all road access points recorded by the Montana Department of Transportation within 10 km of the park entrance station in Gardiner, MT. Bison hunting is concentrated along the roadway as bison migration largely occurs along the south side of the Yellowstone River at the park boundary. Adult male bison can weigh over 750 kg during the hunting season (Yellowstone Bison Office, National Park Service, unpublished data), so the effort required to pack a harvested bison back to the road is great and is avoided by hunters when possible. We created the bison hunting polygon (Fig. 8) with a 1 km buffer around the Old Yellowstone trail and Highway 89 from Gardiner, MT, to the cattle grate at the south end of Yankee Jim Canyon, which limits the northward

movement of bison. We removed a 500 m buffer around the Gardiner landfill and sewage treatment ponds from both hunting regions to minimize the confounding effect of the consistent resource, which lies just within the border of both hunting regions.

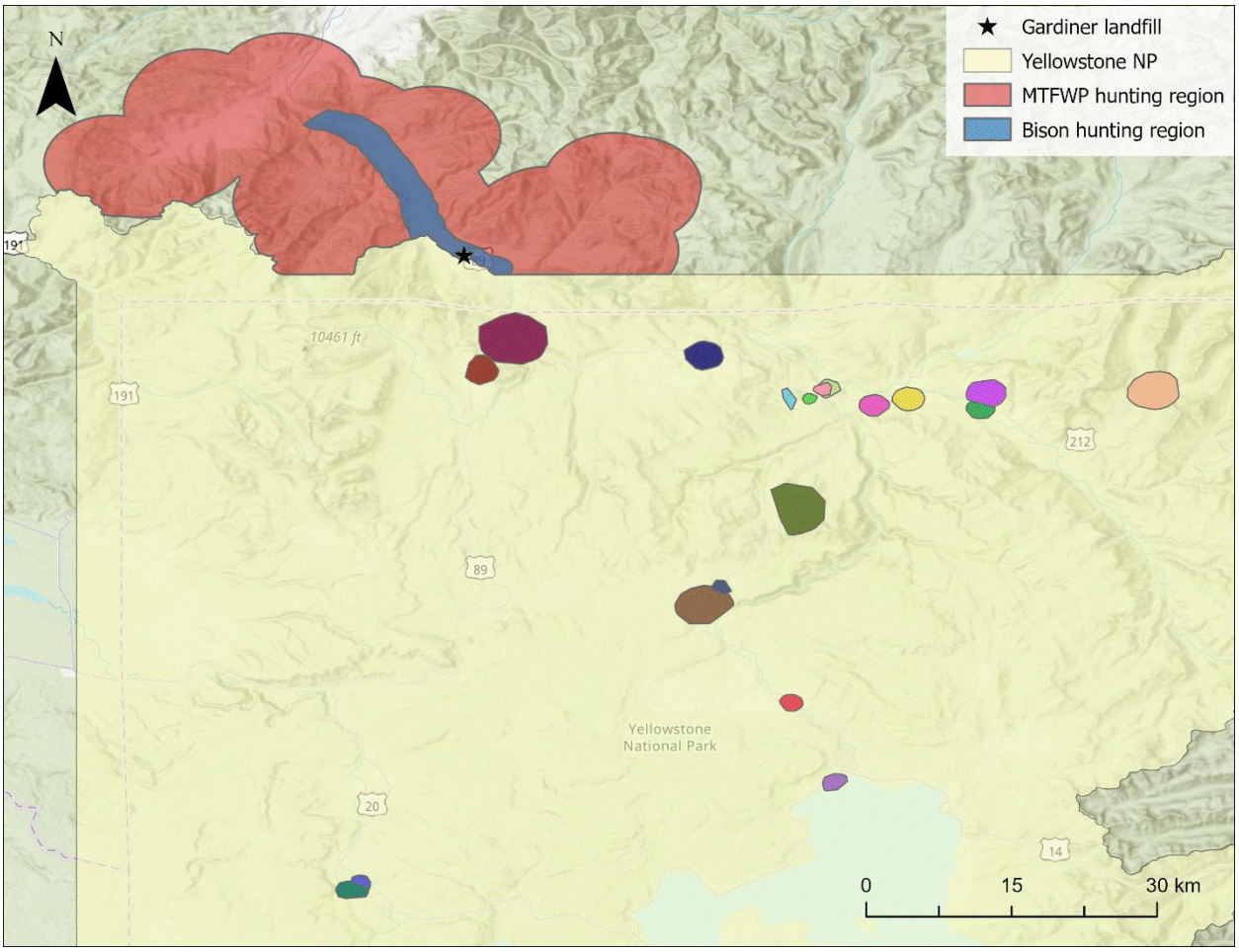

Figure 8. Map of Yellowstone National Park showing the locations of tagged raven territories as colored polygons inside the boundaries. The MTFWP (red) and bison (blue) hunting regions are highlighted outside the northern boundary of the national park. Hunting occurs in the MTFWP region throughout the rifle hunting season and in the bison region after the end of the MTFWP rifle hunting season until March 30. The star marks the Gardiner, MT, landfill and water treatment plant.

3.3.2 Tracking raven movement

We tracked common raven movements in and around Yellowstone National Park between October 2019 and March 2024. We captured ravens between October 2019 and January 2024 with remote-controlled net launchers (Coda Enterprises, Ltd) using various anthropogenic foods and carrion as bait under UW

(3077–01) and NPS (IMR_YELL_Loretto_Raven_2018.A1) IACUC protocols. We opportunistically captured territorial ravens in large feeding groups with vagrant ravens and as targeted efforts at territories along the road within Yellowstone. We fitted solar-powered GPS data loggers (e-obs GmbH; Bird Solar UMTS, 25 g) to each bird using Teflon harness straps (total assembly weight <4% body mass). The GPS data loggers recorded locations every 30 minutes during daylight hours when battery voltage exceeded 3,900 mV, and hourly when between 3,900 and 3,700 mV. No locations were recorded when the battery voltage was below 3,700 mV. Location data were downloaded from the GPS data loggers via Bluetooth to a hand-held receiver or uploaded directly to a Movebank database through a 3G cell network connection.

We determined a raven's territorial status by examining its movements during the breeding season when movements were restricted compared to non-breeders (Webb et al. 2011). We confirmed this in most cases by observing nesting attempts. Four ravens that were non-breeders at the time of capture transitioned into territorial individuals during the study period. We removed male ravens when both birds in a territorial pair were tagged to avoid pseudoreplication because raven pairs travel together during the winter while foraging (unpublished data). We observed that males had fewer days with successful fixes and a lower daily fix rate than females because their longer feathers more frequently covered the solar panel, preventing charging and resulting in lower battery levels. We only retained GPS data between dawn and dusk, as defined by the R package suncalc (version 0.5.1; Thieurmel and Elmarhraoui 2022).

3.3.3 Raven daily movement decisions

We considered our dependent variables to be binary variables if a raven left its territory and if a raven visited the hunting regions each day. To determine if a raven left its territory, we first defined the spatial boundaries of each territory. We determined a raven's territory location and size by creating a 90% minimum convex polygon (MCP) using the package adehabitatHR (version 0.4.22; Calenge 2024) in R (version 4.5.1; R Core Team 2025) from GPS points collected during the breeding season (May - July). We used a less inclusive 90% MCP to remove excursive movements made after nest failure when adults were free to move widely (Fig. 8). To counter the potential underestimation caused by using a 90% MCP, we determine that a raven stayed on its territory if all locations on that day were within 1 km of the 90% MCP boundary.

We defined a visit to the hunting region as ≥1 GPS point within the season appropriate hunting region polygon. The MTFWP hunting region was active for the duration of the MTFWP hunting season, and the bison hunting region was active from that date until March 30th. We removed days where GPS points represented fewer than 5 daylight hours as the data may have been insufficient to detect movement from the territory or to the hunting regions.

3.3.4 Wolf acquired carrion availability

We determined the location and temporal extent of carrion used by wolves using the output of a random forest algorithm developed by Binder et al. (2026) that predicts the location of carcasses from wolf movement, timing, and landscape features (Appendix C: Fig. S1). The model makes no determinations about the prey species or cause of death and functions optimally during the winter study periods performed by the Wolf, Cougar, and Elk Project (November 15 – December 15, March 1 – 30; hereafter early and late winter, respectively). We removed wolf-kill sites identified by the predictive model that were within a hunting region during the hunting season, as ravens would already be classified as visiting the hunting region. Each wolf kill remained active from the beginning of wolf use until 1 day after the last wolf GPS point as direct observations of wolf kills had ravens returning to the site for an average 1.2 days (unpublished data). This additional day accounts for the continued availability and use of the carcass after wolves have abandoned it. We defined the kill availability as a 1 when a wolf kill was active within 1 km of a raven's 90% MCP that day, otherwise 0.

3.3.5 Wolf kill visits

We defined a wolf kill visit by a raven each day as ≥1 GPS points within 500 m of an active wolf kill each day. Given that ravens using a carcass may travel away from the site for short periods of time to cache or perch, we use this distance to better capture that the raven is aware of the resource. Wolf kills within 1 km of their 90% MCP were considered to be inside the territory, otherwise they were considered outside the territory.

3.3.6 Wolf kill density

Ravens holding territories where wolf kills are frequent may remain on their territories when a kill is not immediately available, as they regularly search such areas (Loretto et al. 2026). Using wolf acquired

carrion identified by the random forest algorithm (Binder et al. 2026), we calculated the productivity of a raven's territory as the average number of carcasses acquired by wolves in the 30-day early and late winter periods across all winters that a raven was monitored on that territory.

3.3.7 Recreational hunting season

We retrieved the MTFWP rifle hunting season dates from the hunting regulations published annually by MTFWP (Appendix D: Table S1). We defined the beginning of the bison-hunting season as the first day on which bison were taken that included a second take within 7 days. Bison hunting then continued until the end of winter (March 30; Appendix D: Table S1). Bison-hunting dates were considered flexible because harvest is influenced by bison movement more than hunting-date regulations for tribal hunters. A single exception was made for the winter of 2023, when the only successful take during the study period occurred on March 24, 2024. Hunting season was defined as a 1 for each day within the time window of the MTFWP or bison hunting seasons, otherwise 0.

3.3.8 Estimating recreational hunting biomass

We calculated the availability of hunter-created biomass using hunter take information for elk and deer during the rifle hunting period from MTFWP for the hunting district 313 (https://myfwp.mt.gov/fwpPub/harvestReports) and bison take from the NPS Bison Office (Yellowstone Bison Office, National Park Service, unpublished data). We adjusted MTFWP annual take estimates to account for daily variation because ungulate migration timing is weather-dependent (Rickbeil et al. 2019). We accounted for daily variation in hunter success by using GPS data gathered from elk radio-tagged by the Yellowstone Wolf, Cougar, and Elk project to determine the proportion of elk that had moved outside the national park boundary and were available to hunters. We scaled this proportion of available elk within the year and applied this to the take values for all ungulate species for that hunting year. Male mule deer were the exception as they were protected during the last two weeks of the rifle hunting season. Bison taken in the Gardiner Basin were recorded by the NPS Bison Office daily during the winter through surveys and communications with NPS law enforcement, private hunters, and game wardens.

We adjusted the final take numbers to account for differences in the weights of each target species with elk as the reference species (1x). All deer species had a 0.3x multiplier and bison had a 2.15x multiplier.

These multipliers were calculated by comparing early winter weights of deer and elk and late winter weights of bison (NPS Bison Office unpublished data; Murphy et al. 1998). We accounted for biomass lingering between days by allowing 25% of the biomass to carry over between days.

3.3.9 Commute distance

Since traveling requires both time and energy, we considered the distances of each raven's territory to the hunting regions (Cowie 1977). We calculated the commute distance for each raven by taking the Euclidean distance from the center of the 90% MCP to Yellowstone's northern entrance station in Gardiner, MT, as that was a central location to both hunting regions.

3.3.10 Seasonal behavioral differences

Territory defense and nest construction are behaviors that breeding ravens perform on their territories in late winter prior to nesting that may impact a raven's decision to leave its territory. We defined all days within the March 1 – 30 study period as a 1, and all days within the early winter study period (November 15 – December 15) were 0.

3.3.11 Social information gathering

Ravens are social animals that can utilize information sharing to locate foraging opportunities (Marzluff et al. 1996). We used the GPS tagged ravens to calculate a proxy for the number of territorial ravens within Yellowstone that are making certain movement decisions. When inside their territory, we considered the proportion of other ravens leaving their territories that day. After leaving their territory, we considered the proportion of ravens who left their territory that then visited the hunting regions that day. These calculations were done separately for each raven by day, so the decision of that raven was not included in the value.

3.3.12 Weather covariates

Yellowstone ravens were previously found to visit human areas outside of Yellowstone most frequently when spring snowpack was deep (Walker et al. 2018). We accounted for potential effects of weather by including snow depth and maximum daily temperature from Mammoth, WY, as covariates (NOAA/National Center for Environmental Information 2025).

3.3.13 Modeling daily movement decision

We created two binomial generalized linear mixed models (GLMM) using the R package *glmmTMB* (version 1.1.14; Brooks et al. 2017) with a random effect for individual. We restricted both models to the 30-day early and late winter study periods as these were the time periods for which the wolf kill predictive model was validated. We used a conditional approach to decompose the commuting process into two distinct decisions. The first model investigates whether a raven decides to leave its territory on a given day with raven *j* leaving its territory on day *i* (*Leave*$_{ji}$ == 1) with probability p_{ji}, such that:

$$Leave_{ji} \sim Bernoulli(p_{ji})$$

$$logit(p_{ji}) = \alpha_{0,j} + \alpha_1 * Visit_{ji} + \alpha_2 * Available_{ji} + \alpha_3 * Biomass_i + \alpha_4 * Hunting_i + \alpha_5 * Density_j + \alpha_6 * Distance_j + \alpha_7 * LateWinter_i + \alpha_8 * Temp_i + \alpha_9 * Snow_i + \alpha_{10} * Social_{ji}$$

where $\alpha_{0,j}$ is a random intercept of raven *j.* The second model is conditional on the raven leaving its territory and investigates if a raven decides to visit the hunting regions. We used the second model to account for the presence of other resources (e.g. wolf kills outside the territory or food in other gateway communities) that may influence a raven's decision. In this model, individual raven j visits the hunting regions on day *i* (*Hunting*$_{ji}$ == 1) with probability ϕ_{ji} conditional on raven j leaving its territory on day *i* (*Leave*$_{ji}$ *== 1)*, such that:

$$(Hunting_{ji} \mid Leave_{ji} == 1) \sim Bernoulli\ (\phi_{ji})$$

$$logit(\Phi_{ji}) = \beta_{0,j} + \beta_1 * Kill_{ji} + \beta_2 * Biomass_i + \beta_3 * Hunting_i + \beta_4 * Distance_j + \beta_5 * Temp_i + \beta_6 * Snow_i + \beta_7 * Social_{ji}$$

where $\beta_{0,j}$ is a random intercept of raven *j*. We considered a covariate to be statistically significant at $p \leq 0.05$ and discuss covariates at $p \leq 0.1$ as having weak evidence of an effect.

Table 3. Data types and descriptions for covariates used in the models for territorial raven movement decisions.

Covariate	Type	Description
Available	Binary	1 indicates if a wolf kill was available within 1 km of their territory each day, otherwise 0
Visit	Binary	1 indicates if a raven had ≥1 GPS point within 500 m of a wolf kill inside their territory each day, otherwise 0
Kill	Binary	1 indicates if a raven had ≥1 GPS point within 500 m of a wolf kill outside their territory each day, otherwise 0
Biomass	Continuous	The daily estimated amount of biomass produced from recreational hunting
Hunting	Binary	1 indicates if the day was within the time window of the MTFWP or bison hunting season, otherwise 0
Density	Continuous	The rate of wolves acquiring carcasses within a raven's territory
Distance	Continuous	The commuting distance between a raven's territory and the hunting regions
LateWinter	Binary	1 indicates if the day is between November 15 – December 15; 0 indicates that the day is between March 1 – 30 March
Snow	Continuous	Daily snow depth of Mammoth, WY
Temp	Continuous	Daily maximum temperature of Mammoth, WY
Social	Continuous	The proportion of other territorial ravens that left their territories or visited the hunting regions each day

3.4 Results

During the winter months (Sep – Mar), we gathered 4741 decision days (mean = 249.5, range = 4 – 653, sd = 180.7) from 19 territorial ravens (12 female, 7 male). Ravens left their territories an average of 66% of days (range = 0 – 94.4%, sd = 23.2%, Fig. 9). After leaving their territory, ravens traveled between 7.4 and 57.5 km (median = 32.6, sd = 12.2) to forage in the MTFWP or bison hunting regions 50.6% of days (range = 0 – 90%, sd = 31.4%, Fig. 9). We never recorded two ravens residing at Old Faithful (7485, 7494; 63 km from hunting regions), the territories farthest from Gardiner, traveling to the hunting regions. Instead, they often traveled to forage in West Yellowstone, MT (Fig. 9, 10). The primary resource available to ravens in West Yellowstone is human refuse, although small amounts of recreational hunting also occur in the surrounding lands. Conversely, other individuals who lived closer to Gardiner (8900, 7495) spent the majority of days at the hunting regions (Fig. 9).

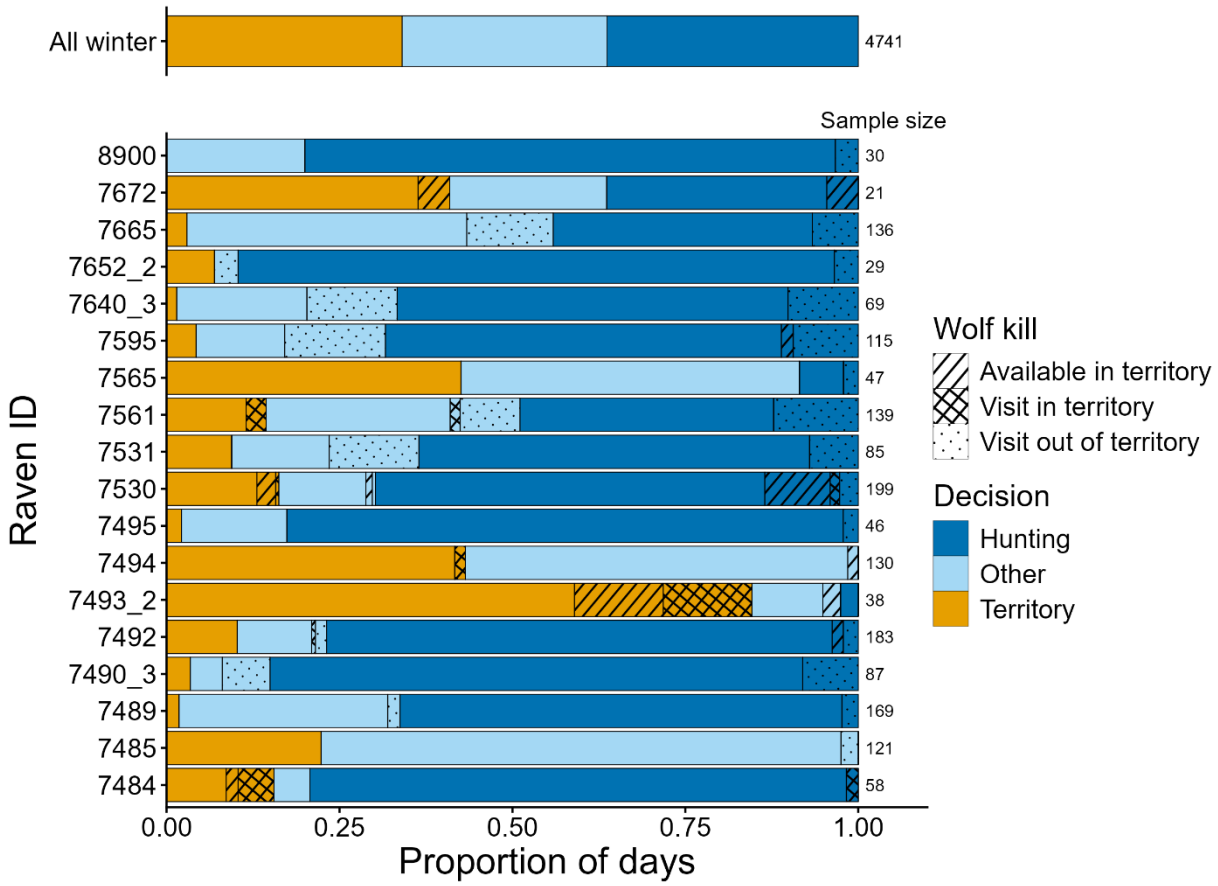

Figure 9. Proportion of decision days when each raven made a particular movement decision. The full winter period shows the mean value across individuals from all decision days gathered between September – March, regardless of year. Individual decisions are shown for the modeling period. When a raven decided to leave its territory, its decision was one of two results: *Hunting* or *Other*. *Hunting* is when a raven visits the hunting regions. *Other* encapsulate all extraterritorial movements that did not result in a visit to the hunting regions. Wolf kill visits inside and outside of the territory are indicated by the pattern on top of the category that represents the final movement decision for that day. The total number of decision days for each raven is displayed on the right-hand side of the plot.

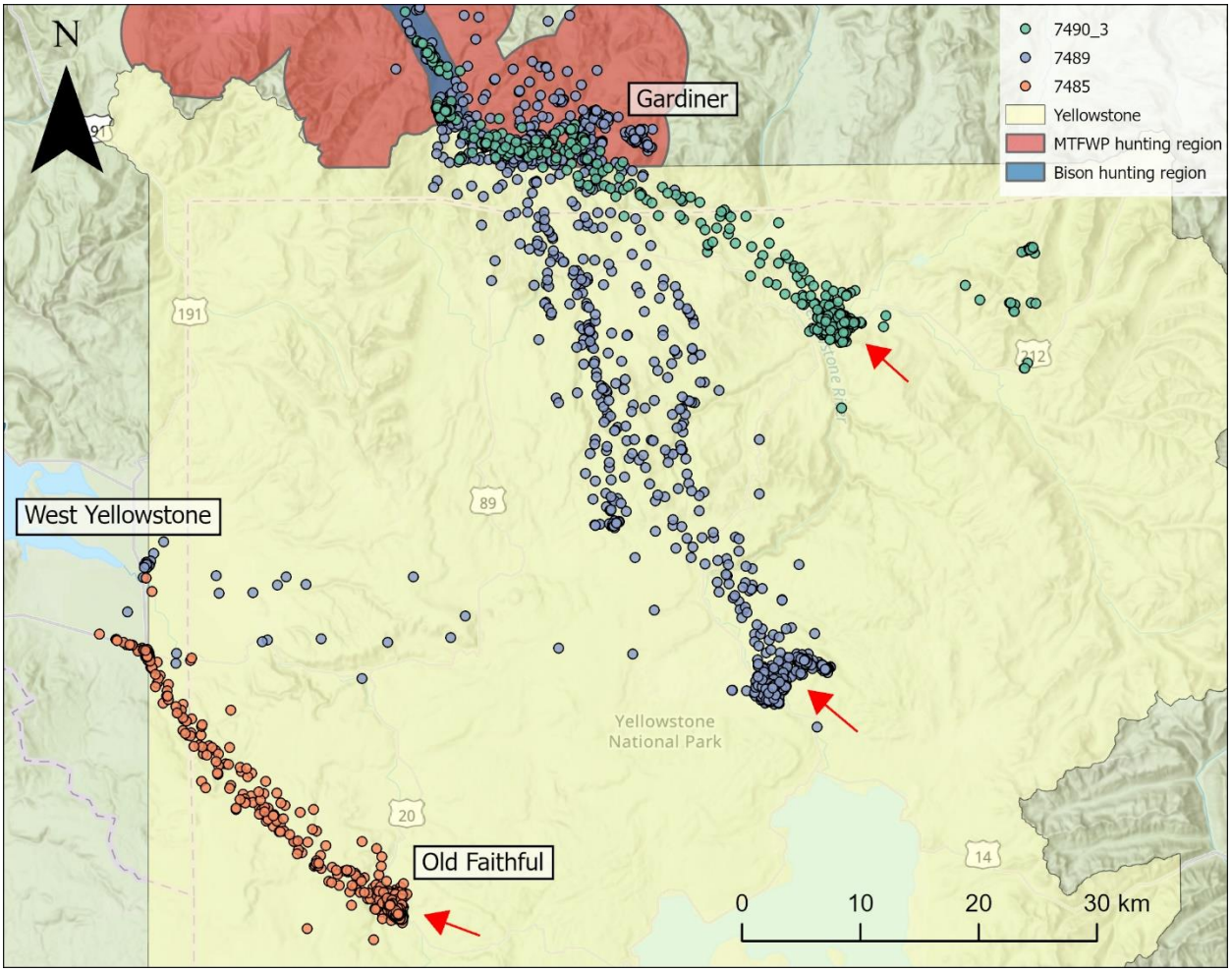

Figure 10. GPS movements of three common ravens from the entire winter (September – March) whose territories vary in distance from the hunting regions. The location of each raven's territory is indicated by the arrow.

Ravens largely remained in their territories until October when ungulate hunting began and the number of visits to the hunting regions increased, at which point, the proportion of days ravens left their territories remained constant throughout the winter (Fig. 11). The number of trips to the hunting regions remained relatively consistent with slight peaks during the primary hunting months of November and March while the centers of activity in the hunting regions shifted in accordance with the location of the primary source of anthropogenic subsidies (Fig. 11, 12). Before hunting began in late October and between hunting seasons in the middle of winter, ravens visiting the hunting regions spent more time at the Gardiner

landfill and sewage treatment ponds (Fig. 12). During the hunting periods, ravens spent the most time in the areas with highest hunting effort for the target species (Fig. 12).

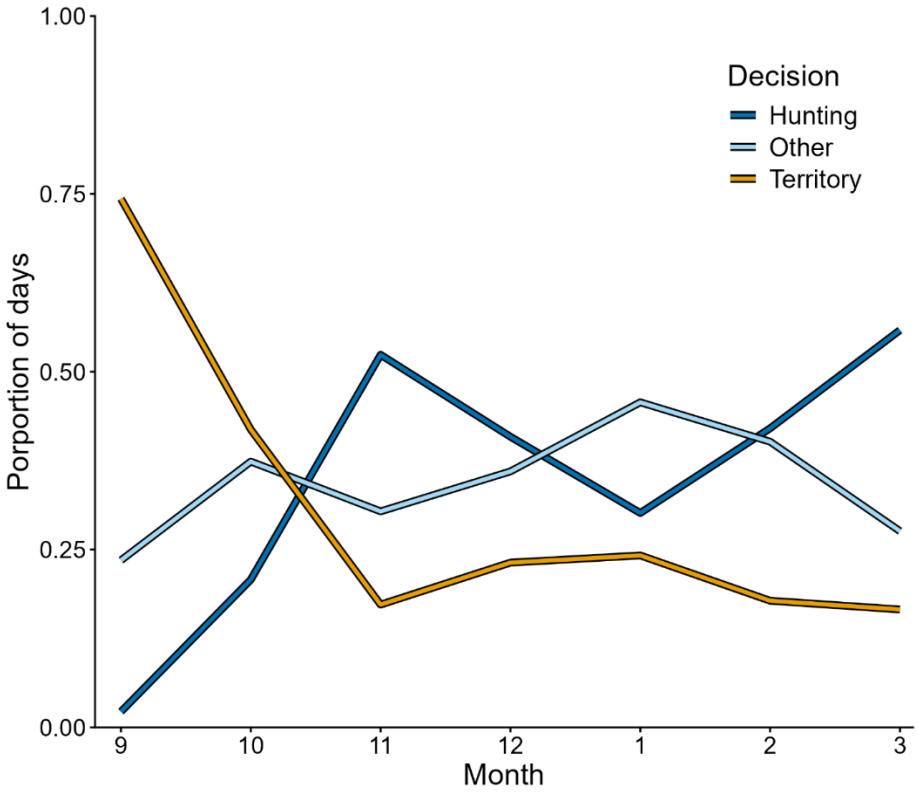

Figure 11. Average proportion of days (between individuals) a raven made various movement decisions during each winter month.

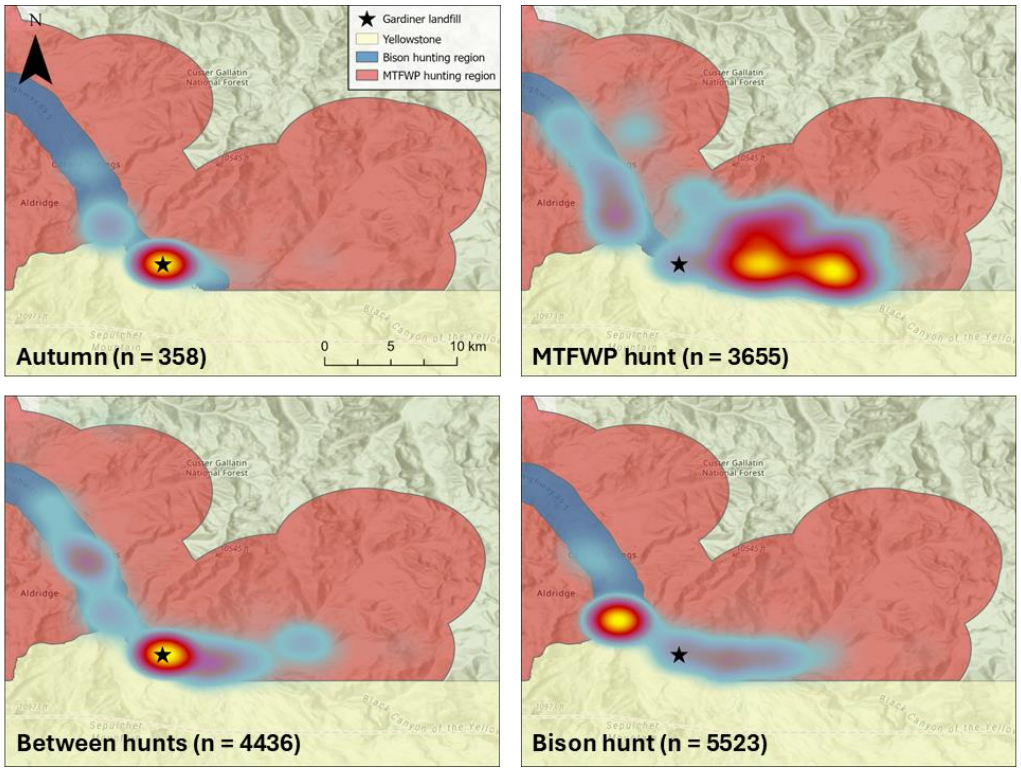

Figure 12. Kernal density estimates of territorial raven GPS points outside of Yellowstone throughout the various winter periods when seasonal ungulate hunting does and does not occur. The entire mapping period is between September 1 and March 31. The *Autumn* period occurs before the start of MTFWP hunting season. The *Between hunts* period occurs between the end of the MTFWP hunting season and the start of active bison hunting. The hunting season dates are listed in the Appendix D: Table S1. The models use a subset of this data from Nov 15 - Dec 15 and Mar 1 - Mar 30.

During the modeling periods when information about wolf kills was available, we had 1702 decision days (mean = 94.6, range = 21 – 199, sd = 56.4). Wolf kills were rarely available to individual territorial ravens, either within or beyond their territory. Raven territories ranged in size from 0.8 – 20.8 km^2 (median = 3.3 km^2, sd = 5.6 km^2) and the median number of days each territory had a wolf kill available was 0 days (range = 0 – 33, sd = 7.9, Fig. 9). Of the 19 wolf kills available within a raven's territory, 10 kills that were detected by observers were identified as elk or bison (Appendix E: Table S1). Kills remained available for an average 3 days (range = 2 – 6, sd = 1.1) with ravens visiting 34% of the available days. 52.6% of kills available within the territory (10) were visited at least once while available (Fig. 9), with the first visit often occurring within the first two days. At six of the carcasses visited, ravens left their territory on the last day of availability, and in three of those cases, the raven visited the kill site before leaving its territory. Six of

the nine kills that were never visited were from one bird (7530) that holds the territory closest to the hunting regions. Wolf kills were visited outside of the territory on a median of 5 days (range = 0 – 29, sd = 10.3, Fig. 9). Most extraterritorial trips (58.2%) to a wolf kill involved the raven investigating the hunting areas as well (range = 0 – 100%, sd = 29.2%, Fig. 9).

3.4.1 Model results

Food availability was the primary covariate that impacted a raven's decision to leave its territory (Fig. 7; Appendix F: Table S1). A raven's probability of leaving its territory decreased by 0.33 (0.31, 0.35) when a wolf kill was visited within 1 km of its territory (Odds Ratio = 0.15, 95% CI: 0.04, 0.55, Fig. 13). However, just the presence of an active kill that was not visited that day did not have a significant effect on the decision to travel beyond the territory ($p = 0.76$). Furthermore, neither hunting biomass nor timing of the hunting season affected a raven's decision to leave its territory ($p > 0.58$). Snow depth was the only weather covariate to show evidence for support with probabilities of leaving their territory increasing with snow depth (OR = 1.2 [0.98, 1.46]). Ravens also left their territories more often when territorial conspecifics were making the same decision (OR = 1.24 [1.07, 1.44]). We found no evidence that a raven's decision to leave its territory was influenced by the distance to the hunting regions, average density of wolf kills in their territory, stage of winter (early or late), or maximum daily temperature (all $p > 0.49$).

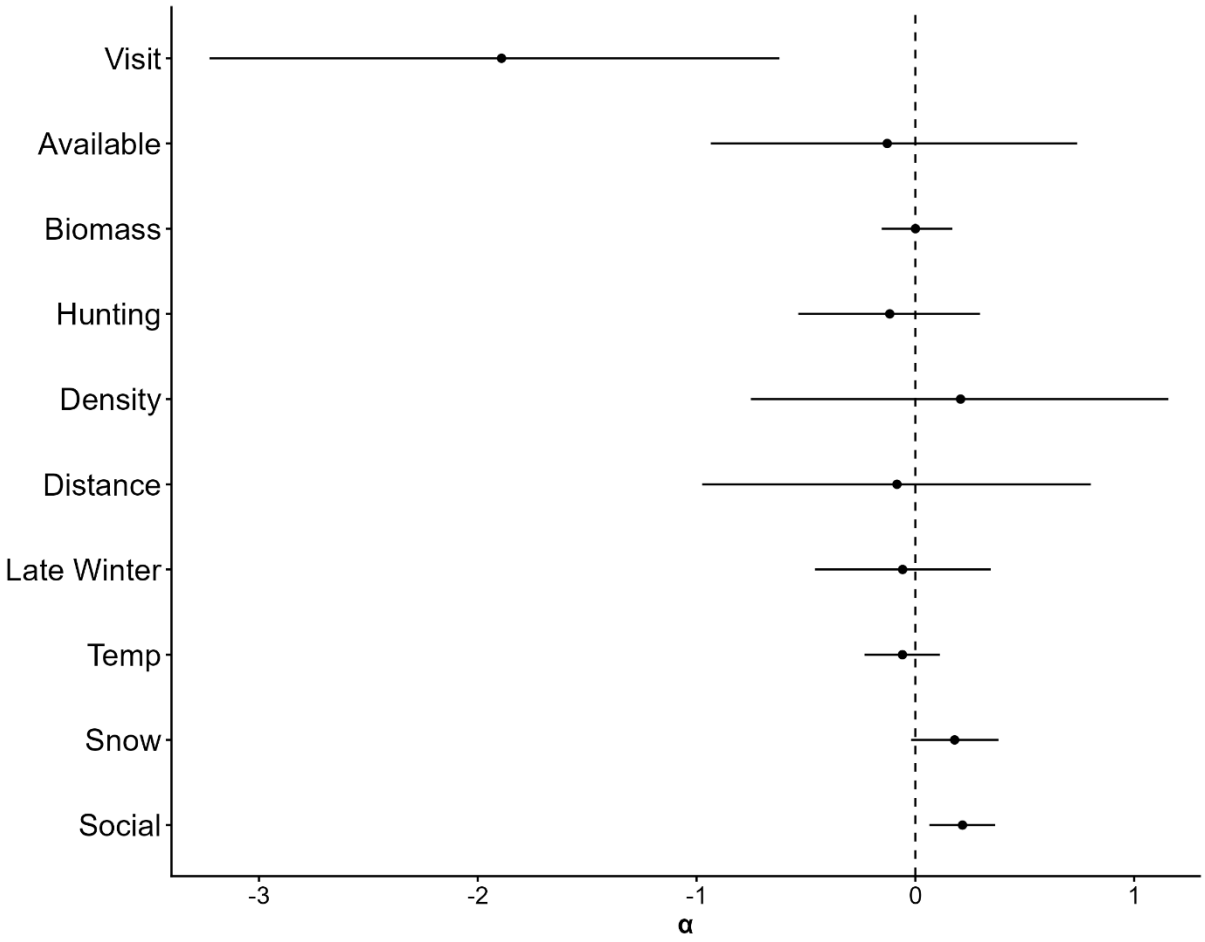

Figure 13. Estimated means and 95% confidence intervals on the logit scale for model parameters from the territory generalized linear mixed model investigating the probability of a raven leaving its territory each day (n_{days} = 1702).

A raven's destination after leaving its territory was influenced by many factors (Fig. 14; Appendix F: Table S2). A raven's probability of visiting the hunting regions increased by 0.27 (0.23, 0.30) during the hunting season (OR = 3.4 [2.34, 4.95], Fig. 15) but was not influenced by the amount of biomass available in hunting areas (p = 0.13). The probability of visiting the hunting area increased by 0.24 (0.21, 0.27) when visiting a wolf kill outside of their territory (OR = 0.33 [0.22, 0.49], Fig. 9). Ravens with territories farther from the hunting area visited hunting with a lower probability than those near the hunting area (OR = 0.17 [0.07, 0.41]). The probability of visiting the hunting area increased as snow depth decreased (OR = 1.32 [1.09, 1.59]) and again, showed no influence from temperature (p = 0.23). Ravens were more likely to

travel to the hunting area when a greater proportion of GPS tracked territorial ravens made the same decision (OR = 1.2 [1.1, 1.5]).

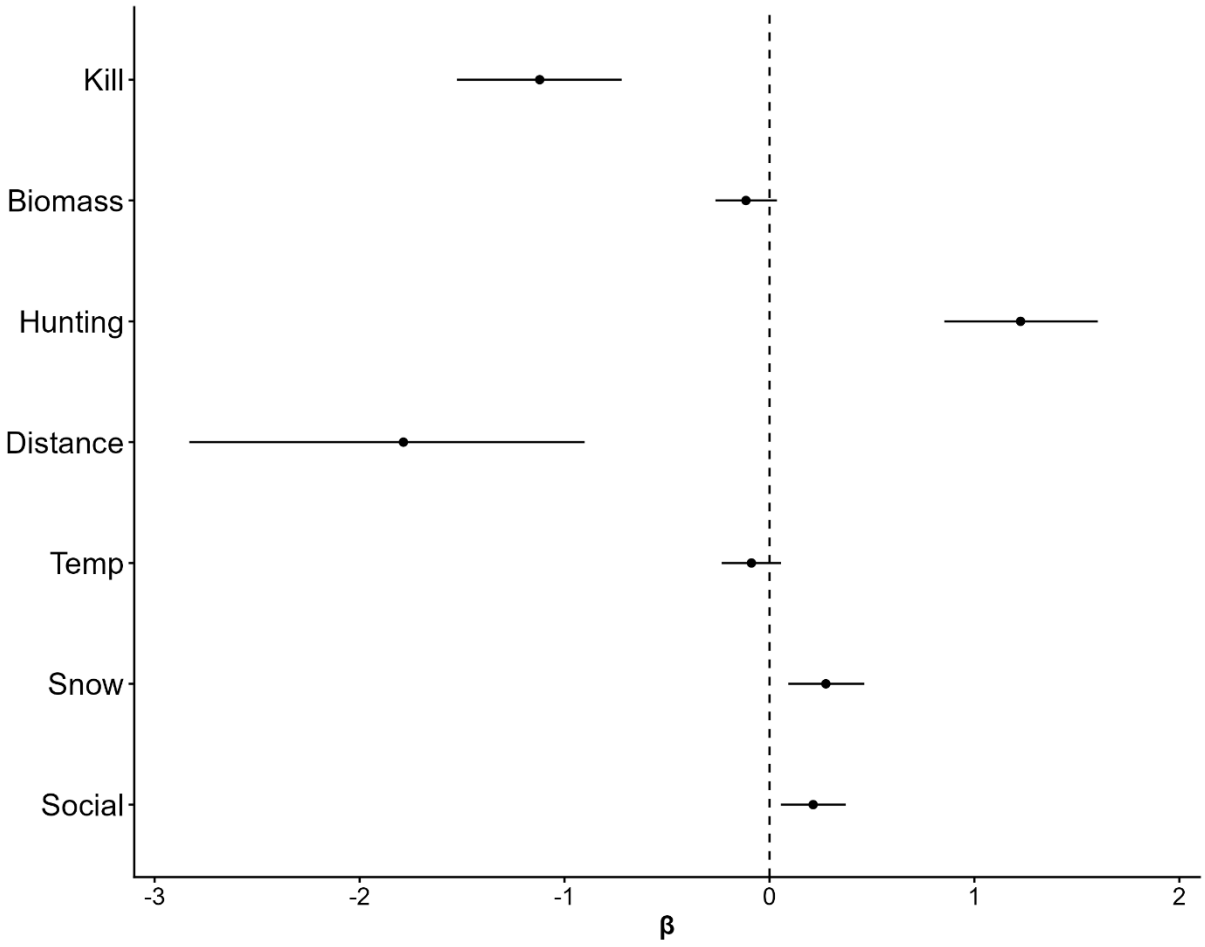

Figure 14. Estimated means and 95% confidence intervals on the logit scale for model parameters from the hunting generalized linear mixed model investigating the probability of ravens visiting the hunting regions on days it has left its territory (n_{days} = 1586).

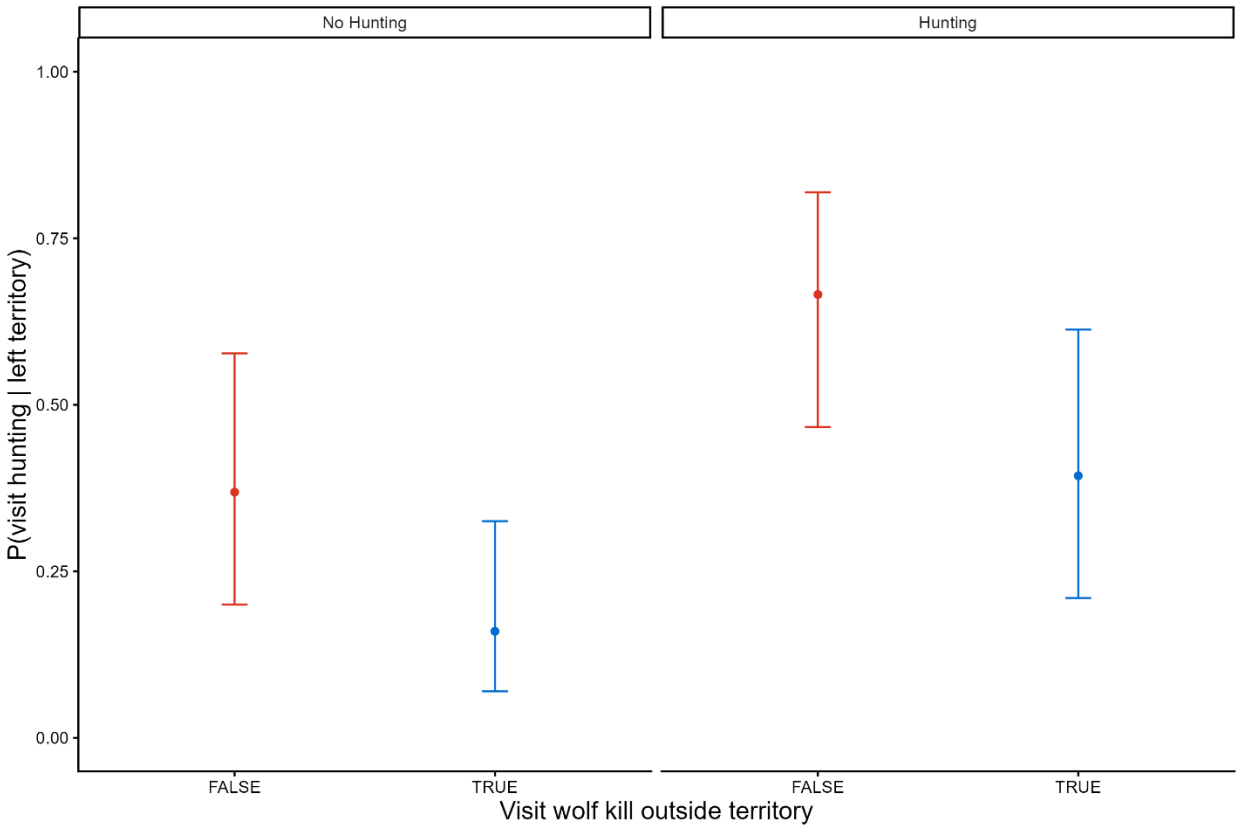

Figure 15. Estimated probability and 95% confidence intervals of a raven visiting the hunting regions based on the timing of the hunting season ($p < 0.001$) and whether they located a wolf kill after leaving their territory ($p < 0.001$). All other continuous scaled covariates are held at 0.

3.5 Discussion

In the wild, animals forage according to optimal foraging theory, reassessing foraging quality and abandoning patches when foraging efficiency drops below a predicted threshold (Amano and Katayama 2009). Ravens in Yellowstone exhibit daily foraging patterns that are consistent with this, maximizing foraging efficiency in response to resource availability while minimizing travel costs. Territorial ravens minimized travel costs by foraging on wolf kills, both within and outside their territories. Ravens that did not locate a wolf kill searched for alternative, distant resources. Travel costs and the likelihood of finding food affected the decisions to leave the territory with ravens traveling to the hunting regions more often during hunting seasons, when carrion is more available, and when their territories were closer to the

hunting regions, reducing travel costs. Adjacent to the hunting region, the landfill and wastewater treatment ponds provided a consistent option for ravens when carrion was unavailable.

Territorial ravens remain place-bound throughout the non-breeding season as they continue to return to their territory each night to roost, similar to a central place forager (CPF). This means that they cannot freely track the best foraging locations like species that move across broad landscapes to track nutrient-dense resources without a home base, such as ungulates following green vegetation or bears moving with salmon spawning (McNaughton 1990, Deacy et al. 2016, Middleton et al. 2018). Unlike CPFs, territorial ravens in the non-breeding season do not have to consider the additional constraints such as load-size or a decreased quitting harvest rate influenced by the need to forage offspring (Charnov 1976, Orians and Pearson 1979). Instead, it is likely they are trying to maximize their personal fitness when deciding which patch within their daily travel range to forage from. This makes the decision to leave their territory simpler than deciding where to travel after leaving the territory, as the only consideration for leaving the territory is a lack of immediate foraging opportunities. Outside of the territory, more variables must be considered to decide the optimal movement based on their understanding of available resources.

We found that wolf kill availability was not significant in predicting if a territorial raven would leave its territory, which is at odds with optimal foraging theory (Hengeveld et al. 2009). Most available kills that were never visited (6) were from one bird (7530) that held the territory closest to the hunting regions. Searching the territory and searching the hunting regions may have similar energy requirements for this individual, which is not reflective of the larger population. Beyond this individual, it is likely that the decision to the leave the territory is more complicated than we captured and involves other factors that can affect a raven's foraging efficiency, such as the predictability of nearby resources, carcass size, the number of wolves and competing scavengers, the remaining biomass, and other non-foraging-related behaviors. Wolf kills of small prey, such as deer, provide less biomass to scavengers, as the pack quickly consumes the prey, leaving little for scavengers (Wilmers et al. 2003a). Even large prey may have little remaining for a raven after days of use by predators and scavengers. Most ravens that left their territory when a kill they had visited was available did so on the last day of the kill's availability. Leaving a wolf kill to forage at recreational hunting areas outside Yellowstone may allow ravens to forage at a greater rate,

as interruptions from competitively dominant scavengers, such as wolves and coyotes, are less likely where humans persecute predators (Wilmers et al. 2003*b*). Measurements of search and handling times using higher fix rate GPS tags and accelerometers would allow further investigation into a raven's decision to leave or remain within its territory.

The complexity of raven decision-making requires consideration of nuanced theory. Optimal foraging theory generally considers a single organism but has been expanded to consider competition and information sharing among social foragers through game theory (Dugatkin and Reeve 2000). Raven decisions may have been influenced by conspecific movement, both within and beyond their territories. Something unexpected given the less social life of territorial versus vagrant ravens (Marzluff et al. 1996). Theory also accounts for varying knowledge of resources, ranging from ignorant to omniscient, with memory playing a role in optimization (Berec 2000). That ravens leave their territories and exploit human hunting grounds during the hunting season is consistent with the use of memory to optimize decision-making. We found snow depth increased the probability of visiting the hunting grounds, which may indicate the use of past experiences when carcasses were more widely available. Recreational hunting is most successful with extensive snow cover as it aids in ungulate detection (Zagata and Haugen 1974). Greater snow depths are also correlated with late winter and harsher winter conditions that can lead to increased ungulate vulnerability to predation and natural mortality (Horne et al. 2019, Kautz et al. 2020). The inclusion and combination of these theory extensions is necessary to capture the real-world decisions made by ravens in a complex system. However, individual variation in decisions still led to large uncertainty across our models.

Yellowstone provides a wide range of patch quality, including resources such as wolf kills (Loretto et al. 2026) and anthropogenic subsidies. Breeding ravens may choose territories near areas of high anthropogenic activity within the park, such as bathrooms, hotels, or frequently used pullouts, which can provide foraging opportunities (Harju et al. 2018). For example, 7493_2 rarely left her territory, in part because of the frequency of wolf kills (Fig. 9). However, her frequent begging from tourists at a parking area in her territory (personal observation) was likely also influential. This was a highly reliable resource with little search time and limited competition. Learning a unique foraging strategy can simplify decision-

making. Conversely, 7485 resided in Old Faithful (orange points in Fig. 10), which is one of the most visited areas during the summer and continues to have residents and tourism throughout the winter. Old Faithful supports many vagrant ravens and multiple breeding territories (including 7494), which increases competition for local resources and likely contributed to 7485 often leaving her territory.

We found that the commuting distance to the hunting region had strong effects on a raven's probability of visiting the hunting regions. This is consistent with optimal foraging theory, where a key idea is that foraging efficiency of a distant patch includes the time and energy spent traveling (MacArthur and Pianka 1966). Some ravens, such as 7485 and 7494, may be unable to access recreational hunting areas given the shorter day length of winter. For territories equidistant from multiple anthropogenic resources (purple dots in Fig. 10), ravens often chose the hunting regions that have greater hunting effort. However, they still occasionally made trips to the alternative anthropogenic sites (West Yellowstone). Ravens were mainly documented using human refuse around West Yellowstone (Ho et al. 2023). Recreational hunting does occur in the surrounding area, mainly targeting bison, although hunter effort is lower than in the Gardiner hunting regions (Yellowstone Bison Office, National Park Service, unpublished data). We did not include this as a potential hunting area as the information about timing and take of ungulates is not well documented. These occasional trips to lower quality patches allow individuals to update their knowledge of distant patches (Smith and Sweatman 1974).

Our sampling of wolf kills and monitoring of ravens was imperfect as some kills and available carrion were not detected. These kills were likely smaller prey species, such as deer, that wolves abandoned more quickly. Although, these instances also yield less biomass to ravens than most detected kills, which were elk. While wolf density, and therefore kill availability, is relatively dense in Yellowstone compared to other ecosystems, very few ravens had wolf kills available to them within their territories. Additionally, the GPS data loggers limited our insights as the fix-rate likely missed visits to wolf kills, especially if the individual did not spend extended periods of time interacting with the resource. This results in an ambiguous interpretation of the wolf kill availability and visit covariates, where it is unclear on which days a raven has knowledge that a wolf kill is within its territory if a GPS point is never recorded at the site.

The rapid expansion of human civilization in the western US led to profound ecosystem change, characterized by the loss of large wildlife populations such as bison and wolves, which altered ravens' winter foraging opportunities. With wolves regionally extinct for nearly 70 years, ravens strengthened their tracking and use of anthropogenic resources. Two decades after the reintroduction of wolves, as predator and prey populations stabilized (Cassidy et al. 2026) and recreational hunting efforts declined significantly (Wright et al. 2006), ravens have returned to a primeval landscape of opportunity, albeit one different from the recent past. Ravens remain the largest scavenger population exploiting carrion created by recreational hunting (Wilmers et al. 2003*b*) and utilize anthropogenic resources more frequently than natural resources during the winter (Ho et al. 2023). Yet ravens have readapted to the restored predator guild by shifting their space use to exploit wolves during winters with greater wolf predation rates (Walker et al. 2018). Perhaps, as throughout the Pleistocene, ravens now select between anthropogenic and natural carrion based on costs and benefits consistent with optimal foraging theory.

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Appendices

Appendix A: Other scavenger species presence at kills

Table S1. The percentage of kills for each predator (n_{wolf} = 32, n_{cougar} = 27) where each scavenger species not included in the main a nalysis was detected on at least one day during the first seven days since the predation event. Nighttime detections are included for cougar kills observed with camera traps.

	Wolf	Cougar
Coyote	87.5% (28)	44.4% (12)
Fox	9.4% (3)	66.7% (18)
Grizzly bear	6.3% (2)	0% (0)
Pine marten	0% (0)	14.8% (4)
Long-tailed weasel	0% (0)	3.7% (1)
Rodent spp.	0% (0)	18.5% (5)
American crow	3.1% (1)	0% (0)
Canada jay	0% (0)	7.4% (2)
Clark nutcracker	0% (0)	18.5% (5)
Mountain chickadee	0% (0)	7.4% (2)
European starling	3.1% (1)	0% (0)
Rough-legged hawk	3.1% (1)	0% (0)

Appendix B: Scavenger count and activity model results

Table S1. Model results from the generalized linear mixed model looking at the impacts of the primary predator on the daily high count of ravens, magpies, golden eagles, and bald eagles at wolf and cougar kills (n = 241). The intercept category is cougar for the primary predator. The model distribution (NegBin or Pois) used for each species is included beside the species name.

	Raven (NegBin)			Magpie (NegBin)			Bald Eagle (Pois)			Golden Eagle (Pois)		
	Est.	Std. Error	p-value	Est.	Std. Error	p-value	Est.	Std. Error	p-value	Est.	Std. Error	p-value
Intercept	-0.963	0.333	0.004	1.066	0.231	<0.001	-3.195	0.517	<0.001	-1.552	0.369	<0.001
Wolf	1.970	0.609	0.001	-0.043	0.472	0.927	0.050	0.879	0.955	-1.336	0.816	0.102
Day	-0.073	0.091	0.426	-0.073	0.053	0.167	-0.093	0.144	0.520	-0.049	0.064	0.444
Tree	0.056	0.230	0.808	-0.391	0.178	0.028	0.428	0.305	0.161	-0.053	0.254	0.835
Roughness	-0.158	0.228	0.489	0.032	0.171	0.852	-0.274	0.328	0.404	0.237	0.253	0.349
Biomass	0.467	0.187	0.012	0.329	0.160	0.039	0.422	0.211	0.046	0.406	0.244	0.096
Wolf * Day	-0.458	0.121	<0.001	-0.123	0.092	0.183	-0.660	0.201	0.001	-0.484	0.169	0.004

Table S2. Model results from the generalized linear mixed model looking at the impacts of wolf kleptoparasitism on the daily high count of ravens, magpies, golden eagles, and bald eagles at cougar kills (n = 190). The intercept category is camera for sample method and FALSE for wolf presence. The model distribution (NegBin or Pois) used for each species is included beside the species name.

	Raven (NegBin)			Magpie (NegBin)			Bald Eagle (Pois)			Golden Eagle (Pois)		
	Est.	Std. Error	p-value	Est.	Std. Error	p-value	Est.	Std. Error	p-value	Est.	Std. Error	p-value
Intercept	-2.748	0.600	<0.001	0.584	0.275	0.033	-5.550	1.724	0.001	-2.079	0.426	<0.001
Visit	2.778	0.817	<0.001	1.028	0.389	0.008	0.598	0.907	0.510	1.149	0.380	0.003
Day	-0.059	0.086	0.494	-0.125	0.047	0.007	-0.147	0.116	0.205	-0.125	0.051	0.014
Observation	1.999	0.962	0.038	-0.172	0.544	0.752	-2.198	2.919	0.451	-0.933	0.752	0.215
Tree	0.714	0.428	0.095	-0.502	0.256	0.050	-0.232	0.835	0.782	-0.200	0.332	0.546
Roughness	0.032	0.414	0.938	-0.022	0.239	0.925	-0.780	1.267	0.538	0.337	0.309	0.275
Biomass	0.441	0.386	0.253	0.547	0.234	0.020	1.767	1.021	0.084	1.012	0.300	<0.001

Table S3. Model results from the generalized linear mixed model looking at the impacts of wolf kleptoparasitism on the foraging rate of ravens, magpies, golden eagles, and bald eagles at cougar kills (n = 201). The intercept category is camera for sample method and FALSE for wolf presence. The model distribution (NegBin or Pois) used for each species is included beside the species name.

	Raven (NegBin)			Magpie (NegBin)			Bald Eagle (NegBin)			Golden Eagle (NegBin)		
	Est.	Std. Error	p-value	Est.	Std. Error	p-value	Est.	Std. Error	p-value	Est.	Std. Error	p-value
Intercept	-3.326	1.009	<0.001	2.757	0.436	<0.001	-8.125	3.321	0.014	-1.482	1.004	0.140
Visit	2.506	1.213	0.039	0.928	0.700	0.185	5.659	3.131	0.071	0.628	0.999	0.530
Day	-0.140	0.131	0.286	-0.478	0.096	<0.001	-0.529	0.461	0.251	-0.463	0.153	0.003
Observation	5.066	1.494	<0.001	0.665	0.870	0.444	-2.491	5.617	0.657	-0.741	1.712	0.665
Tree	1.243	0.662	0.060	-0.632	0.409	0.122	0.128	1.489	0.932	-0.895	0.753	0.234
Roughness	-0.337	0.618	0.586	-0.093	0.393	0.812	-1.539	2.713	0.570	0.479	0.684	0.484
Biomass	1.076	0.600	0.073	1.237	0.394	0.002	2.990	2.212	0.176	2.141	0.775	0.006

Appendix C: Wolf acquired carrion availability

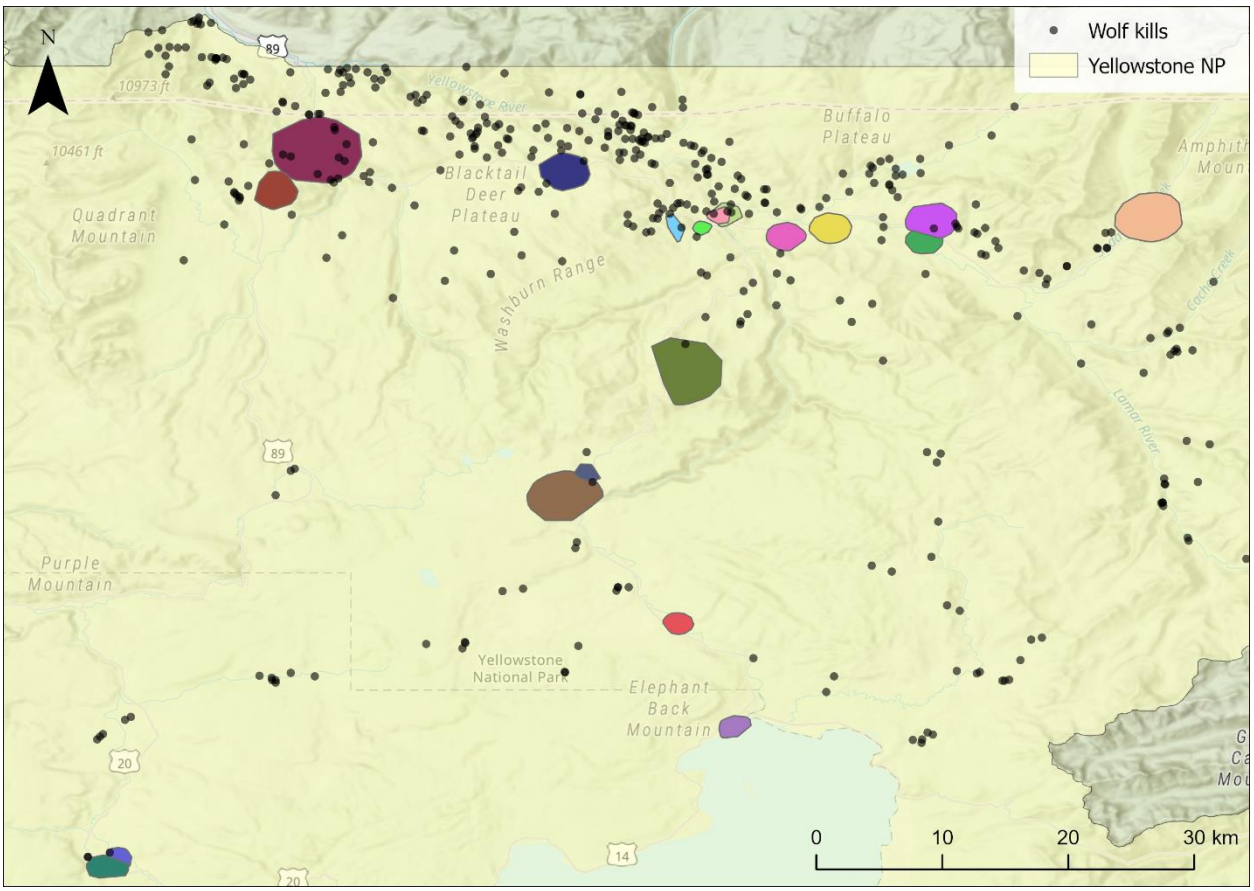

Figure S1. Locations of wolf acquired carrion identified by the random forest predictive model (Binder et al. 2026).

Appendix D: Hunting season dates

Table S1. Start and end dates for the MTFWP and bison hunting seasons for a given winter (e.g. winter of 2019 is from November 2019 – March 2020).

	MTFWP		Bison
Winter of	Start date	End date	Start date
2019	10/26/2019	12/1/2019	2/23/2020
2020	10/24/2020	11/29/2020	1/25/2021
2021	10/23/2021	11/28/2021	3/22/2022
2022	10/22/2022	11/27/2022	12/8/2022
2023	10/21/2023	11/26/2023	3/24/2024

Appendix E: Prey species of kills available within raven territories

Table S1. Species, sex, and age of carcass available to ravens within their territory.

	Elk	Bison	Unknown
Adult Female	4	1	-
Adult Male	3	0	-
Calf	2	0	-
Unknown	0	0	9

Appendix F: Raven movement model results

Table S1. Model results from the binomial generalized linear mixed model looking at the impact of covariates, including requiring ravens to visit wolf kills sites, on the probability of ravens leaving their territory daily (n_{days} = 1702).

	Est.	Std. Error	p-value
Intercept	2.316	0.444	<0.001
Visit	-1.892	0.660	0.004
Available	-0.129	0.424	0.761
Biomass	0.000	0.082	0.999
Hunt	-0.117	0.212	0.580
Density	0.206	0.456	0.651
Distance	-0.084	0.423	0.842
Season	-0.058	0.205	0.775
Temp	-0.059	0.088	0.499
Snow	0.179	0.102	0.078
Social	0.215	0.077	0.005

Table S2. Model results from the binomial generalized linear mixed model looking at the impact of covariates on the probability of ravens visiting the hunting areas surrounding Gardiner, MT when they choose to leave their territory daily (n_{days} = 1445).

	Est.	Std. Error	p-value
Intercept	-0.537	0.433	0.215
Visit	-1.121	0.205	<0.001
Biomass	-0.115	0.076	0.130
Hunt	1.225	0.191	<0.001
Distance	-1.786	0.455	<0.001
Temp	-0.088	0.074	0.234
Snow	0.275	0.095	0.004
Social	0.213	0.081	0.008