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CALIFORNIA CONDOR FEEDING HABITAT, VIGILANCE, AND COMPETITION WITH AVIAN SCAVENGERS IN SOUTHERN UTAH, USA

by

Alex Blanche

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

S. Nicki Frey, Ph.D. Major Professor	Michael Conover, Ph.D. Major Professor
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UTAH STATE UNIVERSITY
Logan, Utah

2024

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ABSTRACT

California Condor Feeding Habitat, Vigilance, and Competition With Avian Scavengers in Southern Utah, USA

by

Alex Blanche, Master of Science

Utah State University, 2024

Major Professors: Dr. S. Nicole Frey, Dr. Michael R. Conover
Department: Wildland Resources

Independent foraging is needed for species reintroductions to be successful, but it can lead to trophic cascades. California condors (*Gymnogyps californianus*) were reintroduced to the Colorado Plateau in 1996, and yearly releases ensure population growth. However, little is known about foraging behavior of condors and their potential competitors. Carrion is a risky food source, and altering behavior can maximize caloric intake while minimizing risk. I investigate habitat selection, vigilance, and interspecific interactions among condors, golden eagles (*Aquila chrysaetos*), turkey vultures (*Cathartes aura*), common ravens (*Corvus corax*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*) on a high-elevation plateau in southern Utah. I measured scavenger activity and habitat variables for 89 carcasses during summer 2022 and 2023 and obtained video of scavenger behavior for 76 carcasses. Condors selected for sparser understory cover, allowing access to lead-free carcasses on sheep bedding grounds where most livestock mortality occurs. Eagles selected for sparse understory cover only when close to roads, and eagles and condors displaced each other. Increased human activity could lead to more intense competition between eagles and condors. The presence of condors at carcasses can force eagles to increase their vigilance, especially when condors arrive in groups. Vultures did not select for any vegetation type, which may buffer against competitive impacts of condors. Vultures prioritize feeding over vigilance when arriving at large carcasses that are likely to attract condors and visit rates of vultures decline after condors have visited a carcass. Ravens, coyotes, and foxes did not display any preferences. Condors, eagles, and vultures responded to different variables, suggesting several tactics to balance energetic demands and safety. Condors arrive shortly after the first scavenger and consume over half the carrion, leaving little for other scavengers. The population densities of eagles and vultures may decline in areas with condors because of additional competition. This study offers insights into the impacts of condor reintroduction and aids the management of condors and their competitors. The potential for changes in scavenger communities may lead to broader changes in carcass distribution on the landscape and could lead to cascades in scavenger, predator, prey, and vegetative communities.

(160 pages)

PUBLIC ABSTRACT

California Condor Feeding Habitat, Vigilance, and Competition With Avian Scavengers in Southern Utah, USA

Alex Blanche

Independent foraging is needed for the reintroduction of a species to be successful, but it can cause cascades in interconnected ecological communities. California condors (*Gymnogyps californianus*) were reintroduced to the Colorado Plateau in 1996, and the population has continued to grow with yearly releases of captive individuals. However, little is known about foraging behavior of condors and their potential competitors. Carrion is a risky food source, and there is a tradeoff between vigilance and feeding. Altering behavior can maximize caloric intake while minimizing risk. Here, I investigate habitat selection, vigilance, and interspecific interactions among condors, golden eagles (*Aquila chrysaetos*), turkey vultures (*Cathartes aura*), common ravens (*Corvus corax*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*) on a high-elevation plateau in southern Utah. I assessed scavenger activity and measured habitat variables for 89 carcasses over the summers of 2022 and 2023 and obtained video of scavenger behavior for 76 carcasses. Condors selected for sparser understory cover, allowing easy access to lead-free carcasses on sheep bedding grounds, where most livestock mortality occurs. Eagles selected for sparse understory cover only when close to roads, and eagles and condors displaced each other when simultaneously present. Increased human activity could lead to more intense competition between eagles and condors. The presence of condors at carcasses can force eagles to increase their vigilance, especially when condors arrive in groups. Vultures did not select for any vegetation type, which may buffer against competitive impacts of condors. Vultures prioritize feeding over vigilance when arriving at large carcasses that are likely to attract condors and visit rates of vultures decline after condors have visited a carcass. Ravens, coyotes, and foxes did not display preference for any variable tested. Condors, eagles, and vultures used different environmental variables to modify their vigilance, suggesting several tactics to balance energetic demands and safety. Condors arrive at carcasses less than an hour after the first scavenger and on average consume over half the carrion, leaving little for other scavengers. The population densities of eagles and vultures may decline in areas where condors occur because of additional competition for carrion. This study offers insights into the impacts of condor reintroduction and aids the management of condors and their competitors. The potential for changes in avian scavenger community composition may lead to broader changes in carcass distribution on the landscape and could lead to trophic cascades in scavenger, predator, prey, and vegetative communities.

DEDICATION

“To art and love and dance and song”

-Nikignik, Hello from the Hallowoods

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Alex Blanche

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CHAPTER I

INTRODUCTION

Scavengers provide important ecosystem services by quickly removing decomposing material and cycling the associated nutrients across a broader geographic area. Decaying animals harbor potentially dangerous bacteria with implications for human and animal health. Avian scavengers are particularly important as they find carcasses more rapidly, consume more decaying biomass, and travel faster and farther than mammalian scavengers (DeVault et al. 2003, Ruxton and Houston 2004). Soaring flight allows avian scavengers to outcompete terrestrial scavengers and can lead to specialization as obligate scavengers (Ruxton and Houston 2004). When obligate scavengers are not present at a carcass, carcass detection and decomposition times are longer (Sebastian-Gonzalez et al. 2013). In Asia and Africa, declines in vulture populations have led to increases in opportunistic mammalian scavengers, especially feral dogs and rats, and longer carcass persistence on the landscape (Pain et al. 2003, Ogada et al. 2012), both of which have negative consequences for adjacent human communities (Markandya et al. 2008).

Unequal competition can contribute to low mammalian scavenger populations, but also can determine the population size of species within avian scavenger communities. Golden eagles (*Aquila chrysaetos*) are able to monopolize carcasses from sea eagles in Norway, and interspecific competition may determine the sea eagles' range and population (Halley and Gjershaug 1998). Black vulture (*Coragyps atratus*) populations have been growing and their aggressive behavior at carcasses and dietary overlap with Andean condors has caused additional concern for the declining condor

(Ballejo et al. 2018). In similar species, spatial, temporal, and behavioral partitioning allows species to co-exist. For example, turkey vultures (*Cathartes aura*) and black vultures are sympatric, but turkey vultures forage individually, in forests, and on smaller carcasses, and arrive more rapidly to carcasses than black vultures do (Byrne et al. 2019).

California condors (*Gymnogyps californianus*) are large, social, obligate scavengers whose reintroduction could lead to cascades within scavenger and predator communities where they overlap. However, a lack of data on condors' habitat and scavenging behavior makes predicting the impacts of condors challenging. This study aims to describe the foraging habitat and behavior of California condors in southern Utah and collect information on competitive interactions with other scavengers.

Historical Distribution and Decline of Condors

During the Pleistocene, California condors inhabited much of North America; their bones have been found in archeological digs in Florida, New York, and Mexico (Steadman and Miller 1987, Carr 2012). As glaciers receded around 10,000 years ago, the diverse assemblage of large herbivores (such as Mastodon, *Mammut americanum*) disappeared, limiting the primary forage of condors. Condors persisted in a condensed portion of their former range across the western United States, restricted by the scarcity of large carcasses and suitable nesting habitat (U.S. Fish and Wildlife Service 2005). For example, condors survived along the Pacific coast of the United States by exploiting marine mammal carcasses, an infrequent resource that continues to be used by condors in Big Sur, California (Chamberlain et al. 2005, Fox-Dobbs et al. 2006).

As whales and seals declined from overharvesting in the 1800s, California condors shifted to terrestrial mammal scavenging, boosted by the increasing cattle industry in the West (Chamberlain et al. 2005). However, during this time, California condors experienced declines from consuming lead from bullet fragments found in game entrails, poaching, and consuming poisoned livestock intended to kill predators (Koford 1953, Meretsky et al. 2000, Snyder and Snyder 2000). Condor distribution continues to be limited to areas with sufficient updrafts and carrion (Poessel et al. 2018).

Current distribution and conservation

In an effort to prevent condor extinction, the US Fish and Wildlife Service (USFWS) began a captive rearing program during the 1980s. In 1987, the last wild California condor was taken into captivity, with a total captive population of 27 individuals (Meretsky et al. 2000). Condors were extinct in the wild for 5 years, but as a result of the captive rearing and reintroduction program, they are now found across California, Baja California, and along the Colorado River across northern Arizona and southern Utah (D'Elia et al. 2015). Current conservation efforts include releases of captive-bred individuals, yearly testing and treatment for elevated blood lead levels, and supplemental feeding of safe carrion.

The California condor population was 560 as of January 2023, with almost 350 free-flying individuals (U. S. Department of the Interior 2023). There are wild fledglings from every flock except the newly established Pacific Northwest population, and populations are also supplemented with releases every year. In March and April 2023, condors in the Arizona/Utah population experienced an outbreak of avian flu, and as of May 2023, 21 condors had died, reducing this population to 95 individuals (U.S. Fish and

Wildlife Service 2023). The rapid spread of avian flu can be attributed in part to the social behavior of condors, as they feed and roost together. Avian flu has not been detected in any other condor population, and the Arizona-Utah population is remote enough that individuals do not disperse or travel to or from other populations.

California condors suffer mortalities primarily from lead poisoning (Meretsky et al. 2000, Finkelstein et al. 2010). When, where and what they forage on influences the levels of lead and other contaminants scavengers are exposed to. This includes gradients such as reliance on coastal vs inland sources of carrion (Kurle et al. 2016), use of proffered carcasses (Bakker et al. 2017), and hunting pressure (Fry and Maurer 2003, Parish et al. 2009, Stauber et al. 2010, Kelly et al. 2011). Species with narrow dietary and habitat breadth are at greater risk from environmental contaminants (Cloyed et al. 2021) and overall extinction risk (Slatyer et al. 2013, Buechley and Şekercioğlu 2016).

A primary conservation effort is the capture and rehabilitation of condors that are affected by lead poisoning. Once recovered, managers release them at one of eight release sites. To ensure successful releases, there are feeding stations associated with each release site, where carcasses free from lead, usually beef or dairy calves (*Bos taurus*), are placed for condors to feed on. In 2005, 45% of the diet of condors in southern California came from dairy calves (Chamberlain et al. 2005, Kelly et al. 2014). Similarly, Baja California does not support a native population of large mammals to scavenge on (Henderson 1964), so condors are still dependent on feeding stations (Sheppard et al. 2013). The only feeding station for the Arizona and Utah population of condors is at the release site in Vermilion Cliffs, Arizona; however, it is rarely used (K. Day, Utah Department of Wildlife Resources, personal communication). No carcasses are proffered in Utah except during attempts to trap condors (K. Day, Utah Department of Wildlife Resources, personal communication). Regardless, it is likely that condors indirectly depend on human activities, as condors did not inhabit Northern Arizona or Utah for 10,000 years before expanding their range when ranching became common (Emslie 1987).

Condor diet

Condors feed primarily on large mammals, including elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), domestic sheep (*Ovis aries*), mules (*Equus asinus* × *Equus caballus*), and cattle (*Bos taurus*), flocking in groups of up to 10 unrelated individuals (Sheppard et al. 2013). California condors will consume carrion that is several weeks old but forgo older carrion if fresher carrion is available (Koford 1953). Despite being generalists that have been recorded feeding on most mammals, they preferentially feed on beef and dairy calves and deer, possibly due to the thinner hides of these individuals (Koford 1953).

In Turner et al. (2017), carcass size attracted different communities of scavengers, with vultures (Cathartidae) more likely at pig (*Sus scrofa*) carcasses than at rat (*Rattus* sp.) carcasses. Changes in carcass species and access points without changing overall size led to changes in condor feeding time but not proportion of time spent feeding (Sheppard et al. 2013). Larger, intact carcasses may be more visible and remain on the landscape longer, increasing the probability of discovery by condors, while small, open carcasses are quickly consumed by vultures. California condors do not prefer carcasses that are already opened but will use existing holes to feed as the birds have difficulty creating new ones (Koford 1953, Snyder N and Snyder H 2005); carcasses that are unopened can also be fed on via natural openings.

Foraging habitat and limitations

Habitat characteristics of carcass locations may determine California condor use. Condors in central California preferentially use coastal dune, deciduous forest, and sparsely vegetated habitats, while avoiding shrublands and evergreen forests, including pinyon-juniper woodlands (Rivers et al. 2014b). Studer (1983) reported primary condor foraging areas as grasslands that support grazing and savannas. However, in Rivers et al. (2014b), grasslands and savannas were used in proportion to availability and not selected for, potentially because these habitats limit the population but not the home range of an individual. Condors also use certain habitats principally for traveling, such as rocky outcrops which produce thermals, but may have low carrion availability.

Disparity between use and availability of carcasses across habitats can result from difficulty detecting and accessing the carcass. For example, Andean condors arrive less often when more black vultures are already at a carcass, although this effect is mediated by habitat and sex of the condor, which may be because black vultures are aggressive and gregarious (Carrete et al. 2010). Black vultures tend to arrive later than turkey vultures at carcasses and are more likely to arrive when other vultures are already present, suggesting that black vultures use other scavengers to detect carcasses (Roen and Yahner 2005). Carcass detection by California condors may also be hindered by dense canopies and tall or thick understories. Carcasses are located by avian scavengers faster when in clearcuts, rather than other forest habitats (Turner et al. 2017). When fires are suppressed, the growth in chaparral impedes condor foraging activities (Studer 1983). California condors can travel over 200 km in a day, but breeding adults primarily scavenge within 50-70 km of their nest (Meretsky and Snyder 1992), so carcasses farther from nesting areas may not be detected.

Safety from predators and disturbance may also limit the areas where condors are willing to feed. Andean condors avoid potentially dangerous habitats, such as flat terrain that hinders takeoff or brush that allows predators to approach unnoticed (Perrig et al. 2023). Similarly, smaller vulture species do not land at carcasses in areas with dense shrub cover that would limit their ability to take off from the ground (Bamford et al. 2009), and are less frequently present and spend less time, with fewer feeding bouts, at mountain lion (*Puma concolor*) kill sites, compared to hog carcasses left by humans (Stangl 2020). Andean condors preferentially forage on mountain slopes for ease of takeoff if predators arrive, despite being able to land on valley bottoms (Donazar et al. 1998). Condors may perceive roads and human activity as unsafe. California condors typically nest far from roads and have not been documented to use roadkill (U. S. Department of the Interior 2021), indicating potential avoidance of roads (Snyder et al. 1986). When approached within 0.4 km by a car, California condors will flush from their feeding site, and Koford (1953) recommends that people give feeding condors at least 0.8 km to avoid disturbance. Even if condors are still willing to feed on a carcass in suboptimal areas, they may display a preference for safer feeding areas by spending more time at or eating a greater proportion of carcasses in safer areas.

Foraging behavior

Behavior at a carcass may be influenced by an individual's characteristics, scavenger group size and composition, and vegetation structure. There is a trade-off between feeding and risk avoidance, which is especially pertinent to condors (Perrig et al. 2023). West (2009) reported that vigilance was higher for males and for older California condors. Although older individuals tend to be more dominant, dominance did not correlate with total time spent feeding, and was weakly, positively correlated to proportion of time spent feeding (Sheppard et al. 2013). Comparing two populations of griffon vultures (*Gyps fulvus*), the population that spent more time feeding also traveled greater distances and was more likely to breed successfully (Fluhr et al. 2021). Snyder and Snyder (2005) predicted that free-flying condors need to eat more than captive individuals, as they have greater energy expenditures, and condors that travel from a far roost site may need to feed for a longer period of time.

Interspecific interactions

In vultures, especially California condors, little is known about foraging tactics and success in competing for carcasses. A common behavior of vultures attempting to claim a kill is to spread their wings over a carcass. With the largest wingspan in North America, the California condor may have the ability to intimidate other vultures and predators at carcasses, especially when feeding in groups. Condors may thus have a disproportionate impact on other predators and scavengers compared to other vultures.

Condors create additional competition for carcasses, as the condor population grows and they return to their original distribution. Predators may kill condors if they are caught at a kill site or may shift feeding and hunting behaviors to reduce interactions with condors. Mountain lions are known to kill competitors when defending kills (Koehler and Hornocker 1991), and since condor reintroductions between 1992 and 2020, 28 California condors have been killed by predators (U. S. Department of the Interior 2020).

Predator and scavenger responses to California condors may include shorter feeding times, increased vigilance at carcasses, and higher kill rates (Hunter et al. 2007, Krofel et al. 2012). Mountain lions in South America have higher kill rates and shorter giving-up times than mountain lions in North America, potentially due to scavenging by Andean condors (*Vultur gryphus*; Elbroch and Wittmer 2013). In southern Utah, the number of lambs killed by predators has not increased since California condor reintroduction, although the proportion of lambs killed by mountain lions has increased (Palmer et al. 2010). Populations of competitors may decline, if costs of behavioral changes associated with condors, such as inefficient feeding due to increased vigilance, cannot be minimized sufficiently.

Diet and behavior of other avian scavengers

In Utah, potential avian competitors of the California condor include golden eagles, turkey vultures, and common ravens (*Corvus corax*). The foraging behavior and dietary overlap between scavengers determines how strongly they may compete and impact each other. Golden eagles tend to prey on leporids but are generalists that will hunt and scavenge on other mid-sized species if rabbits are less abundant, and generally have higher variation in diet in mountainous ecosystems (Bedrosian et al. 2017). Turkey vultures are generalist scavengers, ingesting a variety of mammals (especially large mammals or those susceptible to vehicle collisions), plant material, and garbage (Hill et al. 2022). Common ravens are generalist omnivores, and although their diet composition varies with their environment (Kristan et al. 2004), vertebrates compose a large portion of their diet (Camp et al. 1993).

Golden eagles in larger groups increase their vigilance, contrary to many other bird species, as intraspecific thievery and attacks are the primary concern rather than predation risk (Knight and Knight). Turkey vultures are more vigilant in wooded habitats than in edge or open, even if turkey vultures were more common in wooded habitat than in edge or open (Roen and Yahner 2005). Thick understory and limited visibility correlate with increased vigilance in turkey vultures (*Cathartes aura*; Roen and Yahner 2005). Andean condors are more vigilant and have higher giving-up densities for carcasses up to 350 m from trafficked roads (Speziale et al. 2008).

Visit times for golden eagles decrease for carcasses with nearby understory cover and are smaller for offal than for whole carcasses (Watson et al. 2019). Raven and vulture roosts have been speculated to be information centers, where naïve individuals can learn about carcass locations by following knowledgeable individuals, which requires carcasses to last for at least 2 days (Ward and Zahavi 1973, Prior and Weatherhead 1991, Buckley 1996, 1997; Marzluff et al. 1996). The quick consumption of carcasses by condors may therefore interfere not only with the availability of carrion for vultures and ravens, but also their ability to return as a group to known patches of food.

Methods to document foraging

Previous studies have used isotopes from wing feathers, grown during the summer, to quantify niche breadth, including carcass species and how this varies across ecosystem gradients, such as urban to rural (Duclos et al. 2020), competitor-rich to competitor-poor (Silverthorne et al. 2020), and availability of anthropogenic carrion (Tauler-Ametller et al. 2018). Even when competing in landscapes with several other species, Andean condors have large niche overlap with competitors, and their coexistence may be due to behavioral, temporal, or spatial partitioning (Silverthorne et al. 2020). Isotopic methods cannot differentiate between these kinds of partitioning. Game cameras allow for finer scale study of habitat, timing, and carcass overlap, as they can be used to collect data from an individual carcass rather than all biomass consumed during a growing season and can be used to collect videos showing behavior while at the carcass.

Examining fecal pellets via hair or DNA analysis is another non-invasive method of diet comparison. Andean condor pellets have been used to quantify reliance on human activities and exotic animals (Lambertucci et al. 2009). However, fecal pellet analyses can overrepresent medium-sized mammals (Mersmann et al. 1992) and individuals cannot often be identified using pellets, hindering efforts to conclude dietary changes from movement patterns, age, dominance rank, and other individual characteristics.

Research justification and future implications

The habitat patches within Utah are different than those elsewhere in the condors' range and have undergone changes in the past decades. Utah lacks coastal habitats and may have a greater area dominated by pinyon pine (*Pinus* spp.) and juniper (*Juniperus* spp.). Aspen (*Populus* spp.) stands have declined significantly due to drought, insects, and changing patterns of frost over the past decades on Cedar Mountain and Deep Creek, Utah, where condors are known to spend the summer months (Worrall et al. 2013). Declining deciduous forests may limit California condor foraging habitat, especially if they yield to denser conifer forests. Conversely, projects to convert juniper forests to shrub and grass communities may benefit condors by increasing grazing and therefore foraging habitats.

Most published research on California condors was based on in California, with little to no information gathered from studying condors in the interior section of their range, namely the Arizona strip, north of the Grand Canyon, and southern Utah. This region is unique in its density of juniper and aspen forests. Different vulture populations have been shown to have different energy budgets (flight, resting, and feeding times) and foraging strategies in response to climate and topography (Fluhr et al. 2021). Previous studies have analyzed condor distribution patterns, which clumps use from both foraging and traveling locations, or behavior at feeding stations, which provides predictable food sources that can change foraging behavior. In my thesis research, I study condor foraging patterns in southern Utah, namely Cedar Mountain and the surrounding area, to examine how habitat, carcass, and individual condor characteristics shape condor feeding behavior and presence at carcasses.

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CHAPTER II

FORAGING SITE PREFERENCES OF CALIFORNIA CONDORS AND OTHER SCAVENGERS

Abstract

California condors (*Gymnogyps californianus*) were reintroduced to Vermilion Cliffs, Arizona in 1996, and their population has continued to grow with yearly releases of captive individuals and successful breeding attempts in the wild. Previous studies on condor foraging habitat have examined locations in California, but little is known about preferences of the Southwest experimental population that resides in Arizona and Utah, or how these preferences overlap with those of other scavengers. Here, I investigate preferences in foraging sites by condors, golden eagles (*Aquila chrysaetos*), turkey vultures (*Cathartes aura*), common ravens (*Corvus corax*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*) on Cedar Mountain, a high-elevation plateau in southern Utah. I assessed scavenger activity, using feeding sign and videos from trail cameras at carcass sites, and measured vegetation and landscape variables for 89 carcasses over the summers of 2022 and 2023. Condors selected for sparse understory cover, which was consistent with the findings of previous studies. Condors also selected for longer distances to cover that predators could ambush from and lower angle of ascent, confirming their wariness in landing at carcasses that present difficulties in taking off. Eagles selected for sparse understory cover only when close to roads, so increased human disturbance could lead to more intense competition between eagles and condors. Vultures were more likely to appear at carcasses set out earlier in the season, which may reflect a scarcity of carcasses

early in the summer. Vultures were adaptable to varying distances to predator cover, vegetation types, and obstacles in habitat. Ravens, coyotes, and foxes did not display a strong preference for any variable tested. The habitat preference of condors allows them to easily access lead-free carcasses on sheep (*Ovis aries*) bedding grounds, which is where most livestock mortality occurs. Similarly, this preference suggests that they may not often encounter deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) shot by hunters, which are rarely in open areas. Eagles may face the strongest competition from condors as their foraging niche overlaps the most, while the relative flexibility of vultures may buffer the competitive impacts of condors.

Introduction

Successful conservation of a population depends on the ability of individuals to independently survive and reproduce despite challenges from predators, competitors, and human disturbance. California condors (*Gymnogyps californianus*, hereafter condor) have 4 free-ranging populations; two in California, one in Arizona-Utah, and one in Baja California, Mexico, all of which are initially established by releasing captive individuals. Arizona and Utah contain native scavenger and vegetative communities that differ from the other release areas, including greater frequency of juniper and deciduous forests in Utah (Howard 1996, Zlatnik 1999). The condor population in Arizona and Utah may therefore select for different habitat, which creates interactions and conflicts with different scavenger species than in other parts of the condor's range. The Arizona-Utah condor population is less reliant on human-offered carcasses than other condor populations (T. Hauck personal communication), and their range is smaller than originally predicted, as the condors have been able to find local carcasses (U. S.

Department of the Interior 1996). As this condor population continues to grow in size but not in range, the competitive pressures of condors on other scavengers may also increase. However, no research has been conducted on the amount of niche partitioning between condors and other scavengers, or on the foraging habitat of condors in Arizona and Utah. Here, I test the variables that influence the presence of different species of scavengers at foraging sites and assess the potential for competition with condors.

Habitat characteristics of carcass locations may determine condor use. Condors in central California preferentially use coastal dune, deciduous forest, and sparsely vegetated habitats, while avoiding shrublands and evergreen forests, including pinyon-juniper woodlands (Rivers et al. 2014). In Kern County, California, Studer (1983) reported primary foraging areas of condors as grasslands and savannas. However, Rivers et al. (2014) used GPS location data from condors in the southern/central California population and found that grasslands and savannas were used in proportion to availability rather than being preferred. The availability of these habitats potentially limit the population's distribution but not the size of an individual's home range. Condor locations may reveal selection for habitats that are not used for foraging. For example, rocky outcrops produce updrafts, which are important to condors, but may have low carrion availability due to a lack of vegetation. Foraging only takes up a short portion of a condor's day (San Diego Zoo Wildlife Alliance Library 2024), but has important impacts on scavenger survival and reproductive success.

Disparity between realized foraging niche and carcass availability across habitats can result from the potential difficulty in detecting and accessing a carcass. For example, black vultures (*Coragyps atratus*) tend to arrive later than turkey vultures (*Cathartes* *aura*) and are more likely to use carcasses when turkey vultures are already present, suggesting that black vultures follow other scavengers to detect foraging sites (Roen and Yahner 2005). Carcass detection by condors may be hindered by dense canopies and tall or thick understories. Carcasses are located by avian scavengers faster when in clearcuts, rather than other forest habitats (Turner et al. 2017). When fires are suppressed, the growth in chaparral impedes condor foraging activities (see Studer 1983). Condors can travel >150 km in a day, and breeding adults primarily forage within 50-70 km of their nest (Meretsky and Snyder 1992), so carcasses farther from nesting areas may not be located.

Safety from predators and disturbance may also limit the areas where condors are willing to feed. Andean condors (*Vultur gryphus*) avoid potentially dangerous habitats, such as steep terrain that hinders takeoff or brush that allows predators to approach unnoticed (Perrig et al. 2023). Andean condors preferentially forage on mountain slopes for quick takeoffs if predators arrive, despite being able to land on valley bottoms (Donazar et al. 1998). Similarly, smaller vulture species do not land at carcasses in areas with dense shrub cover, which limits their ability to take off from the ground (Bamford et al. 2009). Turkey vultures are present less often and spend less time, with fewer feeding bouts, at mountain lion (*Puma concolor*) kill sites, compared to hog (*Sus scrofa*) carcasses left by humans (Stangl 2020). Condors typically nest far from roads and only infrequently use roadkill (U. S. Department of the Interior 2021), indicating potential avoidance of roads (Snyder et al. 1986). When approached within 0.4 km by a vehicle, condors will flush from their feeding site, and Koford (1953) recommends that people give feeding condors at least 0.8 km to avoid disturbance.

In Utah, potential avian competitors of the condor include golden eagles (*Aquila chrysaetos*; hereafter eagle), turkey vultures, and common ravens (*Corvus corax*). The foraging behavior and dietary overlap among scavengers determines how strongly they may compete and impact each other. Eagles tend to prey on leporids but are generalists that will hunt and scavenge on other mid-sized species if rabbits are less abundant (Bedrosian et al. 2017). Additionally, they generally have higher diet variation in mountainous ecosystems (Bedrosian et al. 2017). Turkey vultures are generalist scavengers, ingesting a variety of mammals (especially large mammals and those susceptible to vehicle collisions), plant material, and garbage (Hill et al. 2022). Common ravens are generalist omnivores whose diet composition varies with their environment (Kristan et al. 2004), but vertebrates tend to compose a large portion of their diet (Camp et al. 1993).

Medium and large mammalian scavengers, such as coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*), may also compete with condors. As mammalian scavengers mostly feed at twilight or nighttime, competition may be temporally segregated, but exploitation competition occurs as one species removes available food resources from the area for the next species. Mammalian scavengers are potentially dangerous to avian scavengers, can disturb feeding condors, and can consume more meat in one visit than birds can. Mammals that are dominant scavengers use avian scavengers to find carrion and subsequently displace them (Kane and Kendall 2017).

Condors were reintroduced to Arizona and Utah in 1996 after a dramatic reduction in population that culminated in their extinction from the wild. When condors were released back into this area, it was unknown how reliant the birds would be on anthropogenic subsidies of carrion at the release site, and proffered, safe carcasses were touted as a way to keep condors safe from lead poisoning. Condors that are more reliant on carrion from release sites have lower risk of lead poisoning in California, where regulations limit the use of lead ammunition (Kelly et al. 2014). However, condors in Arizona and Utah tend to find their own carcasses rather than foraging on safe carcasses set out for the condors (Hunt et al. 2007), and lead poisoning from consuming carcasses of mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) shot by hunters continues to be an issue (Parish et al. 2007, Bakker et al. 2024). In Arizona, condors forage primarily on public land (Walters et al. 2010); while in Utah, condors are found within a mixture of private sheep (*Ovis aries*) pastures, Dixie National Forest, land managed by the Bureau of Land Management, and Zion National Park. Changes in livestock abundance and management influence the foraging range and amounts of safe carrion available, and therefore persistence of condors in these areas (Studer 1983). As large obligate scavengers, condors may dominate smaller scavengers, potentially causing an adverse impact on native scavengers. Researching the niche overlap among scavengers is crucial to understanding the impacts of condors on their competitors. If there are strong similarities in habitat preferences of condors and another scavenger at foraging sites, that scavenger may face more competitive pressure from condors. The overlap in foraging habitat between condors and other scavengers is unknown in Utah, as no studies have examined the foraging habitat of condors. In this study, I aim to address this issue by evaluating the effect of landscape, vegetation, and carcass characteristics on scavenger presence at foraging sites. Specifically, I will test the hypotheses that condors and other avian scavengers are more likely to forage on carcasses that are located where mammalian scavengers can be detected at a distance, angle of ascent is shallow, understory coverage is sparse, and human disturbance is less common.

Methods

Study Area

Cedar Mountain is a high-elevation (>2500 m), primarily private plateau used as summer sheep pastures in Iron County, Utah (Fig. 2.1). Presence of larkspur (*Delphinium* spp.) restricted grazing activities to sheep rather than cattle (*Bos taurus*) because this plant is toxic to cattle. The relatively cool temperatures and late growing season of the mountain allowed the sheep to graze throughout the summer and early fall (June – September). California condors used Cedar Mountain coinciding with sheep grazing activity at high elevations in the region (Palmer 2009). On Cedar Mountain, condors primarily fed on sheep carcasses, due to their high availability compared to native wildlife species (T. Hauck, Peregrine Fund, personal communication). Vegetative communities were predominantly grassland and aspen (*Populus tremuloides*) forests, with less frequent shrublands (principally *Artemisia tridentata*) and aspen-conifer or coniferous forest (*Abies lasiocarpa* and *Pseudotsuga menziesii*; Rogers et al. 2010, Britton et al. 2016). I monitored condor use of sheep carcasses with trail cameras on 9 pastures spanning 1900 ha, owned by 7 private landowners. Pastures were chosen based on a map of previous condor locations, as well as landowner permission, presence of sheep, and location on the center of Cedar Mountain. I monitored carcasses from May to September in 2022 and 2023. As of July 2023, the Arizona-Utah population of condors included 95 individuals, although not all individuals used Cedar Mountain.

Study design

At the beginning of each field season, I consulted with sheep producers and confirmed where the sheep bedding grounds were going to be on each pasture, as depredation most commonly occurred at twilight or nighttime, when sheep are on or near the bedding grounds. Over the summers of 2022 and 2023, I systematically searched for sheep mortalities on pastures by walking along sheep trails from bedding areas to resting areas (similar to Palmer et al. 2009). I also investigated any reports of mortalities from ranchers and shepherds. I found fewer sheep carcasses than expected during the summer of 2022; therefore, I also searched for and collected mule deer carcasses as I drove along Utah State Route 14 on the ~60 km section between Cedar City and Duck Creek Village, Utah, and I obtained locations of roadkill from Utah Division of Wildlife Resources (UDWR). These carcasses were randomly distributed across the study area, as described below. I also distributed ewe and lamb carcasses obtained from ranchers within the study area. In 2023, I obtained lamb carcasses from sheep producers during spring lambing (April-May) and froze them in anticipation of summer fieldwork. I primarily relied on setting out lamb carcasses rather than expanding efforts to search for mortalities in pastures.

When I found sheep carcasses in pastures, I usually monitored them where they were found. I only moved carcasses found on Cedar Mountain when they were <10 m from a public road. To determine where to place supplemental carcasses, I used ArcGIS (ESRI 2023) to view pastures where I had landowner permission to access. I used rasters from the Landscape Fire and Resource Management Planning Tools Project (with 30 m resolution; LANDFIRE 2020) to collect data of existing vegetation type. I combined existing vegetation types broadly into 10 major categories following Rivers et al. (2014) to create classifications relevant to condors and which encompassed vegetation types likely to be encountered. These categories included deciduous forest, evergreen forest, savanna, grassland, sparse vegetation, shrubland, modified land, wetland/riparian, agriculture, and unsuitable habitat (e.g., cities and open water). This classification method was similar to those used in Stoms et al. (1993) for condor sightings. I used stratified random sampling within accessible areas, defined as slope <45°, <5 km of a road, and >100 m from any buildings, to randomly generate an equal number of points across vegetation types. Points also had to be >200 m from each other. These random locations were used when placing carcasses within a pasture. Pastures were rotated through to avoid attracting predators to an unnatural abundance of food. In 2022, when I found roadkill on the state highway, or obtained carcasses from producers, I relocated it as soon as possible to the next random location on Cedar Mountain. Every week over the summer of 2023, in addition to locating naturally occurring sheep carcasses, I set out >2 carcasses, each consisting of ≥1 frozen lambs (total initial weight 3.2 - 20.4 kg). At any one time, only <7 carcasses were available to scavengers, and due to quick decomposition and consumption rates, often 2 - 4 carcasses were active simultaneously. Carcasses that I set out were placed >2 km from the nearest active carcass to avoid overlap in detection by scavengers based on proximity (similar to Speziale et al. 2008).

I used trail cameras (Campark T20 Mini Trail Camera, Campark Electronics, Portland, OR) placed on trees, fence posts, or staked metal poles, approximately 1 m off the ground (the average scavenger height) to record visits from scavengers. I scheduled cameras to take 30-s videos with 5-s intervals whenever motion was detected, with low sensitivity to minimize videos of vegetation moving with wind. I used 16-GB and 64-GB SD cards (SanDisk, Milpitas, CA) in the cameras. I placed 2 cameras on each carcass, one ~3 m away and one ~5 m away, at 90° from each other, to avoid missed scavenger visits from size differences, scavengers dragging carcasses in different directions, and camera failure. I tied carcasses with a cable snare and staked them into the ground with 45-cm-long steel stakes to prevent the carcass from being dragged out of the cameras' frame.

I checked camera batteries and SD cards at least weekly and replaced these as needed. Trail cameras were continuously active at carcasses until carcasses were at least 75% consumed, had been out for at least 7 days, or reached such an advanced stage of decay that most mammalian and avian scavengers would not feed on the carcass due to putrefaction. I visually estimated the proportion of the carcass consumed, size of openings in the carcass, stage of decay, and eagle and condor sign during these checks. Eagle feeding sign included broken smaller bones and plucked wool around sheep carcasses. Condor sign included the hide turned inside-out from the skeleton, intact skin and bones picked clean of meat, large feathers scattered nearby, and trampled vegetation around the carcass. Both species' sign were consistent and conspicuous, so that I could easily determine both presence and absence, especially when combined with camera footage. I noted fox and turkey vulture sign when present but did not report absence when sign was not present. Fox sign included fresh canid feces on the carcass and chunks of flesh eaten with broken bones. Vulture sign consisted of small openings in the carcass, bones neatly picked clean of tissue, and fresh avian scavenger droppings without associated condor or eagle sign. Because sheep herders on the mountain usually used domestic dogs (*Canis lupus familiaris*) during their operation, coyote presence and absence was determined from videos only, because coyote and dog sign looks similar. If sign was ambiguous without video confirmation of scavengers, I reported scavenger presence as missing. From feeding sign and video, I determined the presence and absence of condors and eagles, as well as the presence of eagles, ravens, foxes, and coyotes.

I monitored carcasses such that at least one carcass was active each week, each placed at a new location. When setting out carcasses, I selected locations so that carcasses were being monitored in different vegetation types at the same time, across multiple pastures. Each pasture had multiple vegetation types, but only up to 2 carcasses were active simultaneously in any given pasture, to keep active carcasses as far apart from each other as possible and to prevent drawing predators to pastures. The availability of vegetation types and the unequal detection and occurrence of natural mortalities skewed how many carcasses were in each vegetation type, but I attempted to select carcass locations to reflect the vegetation types on Cedar Mountain. For example, wetlands and agriculture are scarce on Cedar Mountain, so they received few carcasses. Similarly, the land type 'modified land' was primarily represented by roads, where carcasses could not be placed due to human activity. Sheep tended to bed down in open areas, and as a result, most mortalities were found in grasslands or sparsely vegetated land cover types.

Effects of vegetation

I measured several potentially explanatory landscape variables at carcass sites. I measured canopy closure at the carcass using a convex spherical densiometer (Forestry Suppliers, Jackson, MS; Paletto and Tosi 2009). I also measured understory density using a Nudd's profile board (Nudd 1977) with 5 stacked 0.5-m-high sections in a random compass direction, and dominant vegetation height (m). Random directions were chosen by spinning the compass dial. Vegetation height was measured every meter along a 15 m long transect in a randomly chosen direction, starting at the carcass. These data were later averaged. At the carcass, I calculated slope and aspect using a compass (Silva Ranger 2.0 compass, Silva, Sandy, UT). Angle of ascent was the minimum angle that birds would have to clear if taking off from the carcass, also measured using a compass in each cardinal direction. At each carcass, I retained the minimum and maximum values; minimum values representing ease of clearing vegetation in any single direction, and maximum values representing difficulty of clearing vegetation from any single direction.

Effect of risk

To assess human activity, I calculated the distance of the carcass to the nearest trafficked and public road in ArcGIS (ESRI 2023). Locations of the carcasses were taken using a handheld GPS unit (Garmin GPSMAP 64x). Trafficked roads were defined as maintained dirt or gravel roads that were used at least weekly, signifying active human disturbance. Public roads were defined as those that were driven on several times each day and were paved or well-maintained dirt roads that had public access. Road layers were downloaded in November 2023 from ArcGIS Hub’s Utah Roads dataset, compiled by the Utah Automated Geographic Reference Center. I removed roads from the layer that were known to be private and only accessible through locked fences to create a public roads dataset.

Finally, I calculated the distance to the nearest mammalian predator cover. I calculated distance to predator cover as the closest distance from the carcass at which a 0.5 m^2 checkerboard could be entirely hidden by vegetation or terrain, imitating the size of a coyote approaching head-on. Vegetation and abiotic obstacles were progressively tested for full concealment, moving further from the carcass in any direction until the board was completely hidden.

Data analysis

I investigated in which habitats condors prefer to forage using vegetation and topographic data. I determined condor preference using a binary variable delineating condor attendance at carcasses in different habitats. All statistical analyses were conducted in R (version 4.2.1, R Core Team 2021) with package “tidyverse” (version 1.3.2, Wickham et al. 2019). I used *t*-tests to evaluate certain variables hypothesized to impact presence of condors, eagles, and turkey vultures at carcasses. For condors, this included distance to predator cover and minimum and maximum angles of ascent. For eagles, this included distance to predator cover and minimum and maximum angles of ascent. For vultures, this included minimum and maximum angles of ascent. However, *t*-tests cannot evaluate several variables together, hence, I employed a logistic regression framework to evaluate variables whenever possible.

Within the available pastures, the data were independent use-nonuse points with random sampling. Therefore, I used a single logistic regression (generalized linear model with family= “binomial” and link= “logit”) to examine what habitat characteristics are important for condor presence or absence (Keating and Cherry 2004, Fieberg and Johnson 2015).

I started each model with all variables, and kept variables based on priority whenever possible. I ran a series of *t*-tests as part of data exploration for every variable’s impact on condor presence (Appendix A: Table A1). All possible variables included ordinal day established, average canopy closure, distance to predator cover, understory cover (as an average and broken up into measures for every 0.5 m of height), slope, elevation, average vegetation height, distance to paved road, distance to all roads, initial weight of the carcass, maximum and minimum angle of ascent, and aspect (separated into northness and eastness). To avoid issues associated with multicollinearity, I conducted Pearson correlation analyses and only kept a single variable when several were correlated with each other, using a cutoff of $r < 0.6$ (Dormann et al. 2013). To avoid overfitting, I limited the number of covariates I was testing to have at least 10 successes (presences) and failures (absences) per variable in the model. I selected the variables that appear in the final model based on the hypotheses most of interest and comparing iterative fits of QQ plots and residuals versus predicted plots using DHARMa (version 0.4.6, Hartig 2022). If models did not display a good fit through simulations, I considered alternative variable combinations and transformations of the variables that were in the model.

I repeated this model building process for each species of scavenger for which I had presence data, namely eagle, turkey vulture, red fox, coyote, and common raven. I tailored models to include the most relevant terms for each species based on prior knowledge of their biology. For example, coyotes may be more sensitive to paved roads due to human disturbance, while ravens may be less sensitive to roads but wary of attending carcasses close to predator cover.

Results

I monitored 39 carcasses in 2022, and 50 carcasses in 2023. I was able to determine presence and absence for condors at 82 carcasses, eagles at 78, turkey vultures at 75, foxes at 70, coyotes at 72, and ravens at 72. Of those, condors were present at 24%

(20/82), eagles 31% (24/78), turkey vultures 57% (44/75), foxes 34% (24/70), coyotes 17% (12/72), and ravens 17% (12/72). Of all 89 carcasses, 83 were fresh enough to deploy cameras, as well as being assessed for previous scavenger activity. Cameras failed after deployment at 7 carcasses, resulting in video monitoring for 76 carcasses during the study.

When checking for collinearity, I found significant correlation between the measures of understory density and angle of ascent, as well as between the taller (1.5 m and up) sections of understory density and both canopy cover and average vegetation height (Appendix A: Table A2). I removed maximum and minimum angle of ascent, average canopy, and all but the lowest section of understory density when average vegetation height was included in the model, to avoid redundancy when testing variables and as effects could not be separated. A-priori, I determined that if there were any outliers that had residual absolute values >3, I would remove them and reevaluate the model (Stoltzfus 2011); however, after creating and testing each model, none had outliers.

Using *t*-tests, condor presence was impacted by distance to predator cover (P = 0.009), maximum angle of ascent (P < 0.001), and minimum angle of ascent (P < 0.001; Table 2.1). After removing variables to avoid collinearity and overfitting, the possible model variables to explain condor presence included average understory cover and distance to the closest paved road. However, only understory cover had a negative influence on presence (P = 0.018; Table 2.2). Every 1-unit increase in average understory cover decreased the odds of a condor appearing by a multiplicative factor of 0.22 (Fig. 2.2).

Using *t*-tests, eagles selected for lower minimum angle of ascent (P = 0.041) but not maximum angle of ascent or distance to predator cover (Table 2.1). In the model to explain golden eagle presence, I included average understory cover, distance to the closest paved road, and an interaction effect between them. The interaction between distance to a paved road and the average value of understory cover (from the ground to 2.5 m) was significant (P = 0.004; Table 2.3). At longer distances from roads, eagles preferred thicker understory cover, and at shorter distance to public roads, eagles preferred less understory cover (Fig. 2.3).

From *t*-tests, turkey vulture presence was not influenced by minimum or maximum angle of ascent (Table 2.1). The model for turkey vulture presence included ordinal day of carcass establishment, distance to predator cover, distance to the closest paved road, average vegetation height, and the lowest section of understory cover. The only statistically significant predictor was ordinal date (P = 0.002, Table 2.4). Turkey vultures had 2.4% lower odds of appearing with each passing day of the season (Fig. 2.4). In the model for raven presence, average vegetation height was the only variable in the model and was not statistically different (Table 2.5).

In the model for coyote presence, distance to the closest paved road was the only variable in the model and was not statistically different (Table 2.6). For foxes, I included average vegetation height and coyote presence. Average vegetation height was slightly different, although not statistically so (P = 0.11). The resulting coefficient was small enough to be negligible, as it indicates a 0.1% increase in odds of a fox arriving with each additional cm of vegetation height (Table 2.7).

Discussion

California condors have been reintroduced to their historic range as 4 distinct populations in southern and central California, northern California, Arizona-Utah, and in Baja California, Mexico. Most studies examining the space-use of condors have focused on individuals in southern and central California. Of the few studies published on condors in Arizona-Utah, most focus on lead poisoning and population dynamics (Emslie 1987, Meretsky et al. 2000, Woods and Heinrich 2007, Green et al. 2008, Parish 2009, Walters et al. 2010). The Arizona-Utah population of condors faces greater threats from lead ammunition than the California populations due to policy differences among states and more frequent foraging on animals shot by hunters. Condors are typically reported to feed on medium to large animals (Wilbur 1972) and while the smallest lambs I set out were 3.5 kg, condors fed on those smallest lambs, perhaps because of other scavengers or scarce nearby vegetation aiding in the detection of these smaller carcasses. As sheep are the most common livestock on Cedar Mountain, condors are accustomed to finding and feeding on smaller lamb carcasses. The vegetation communities available to condors for foraging are different across the 4 distinct populations. For example, in Rivers et al. (2014), condors in central California selected for coastal dune and deciduous forest, but that may not be applicable to Utah given that coastal environments do not exist there. On Cedar Mountain, Utah, the predominant forest type is aspen, which is rare in southern and central California.

Previous studies have focused on individual condors, rather than carcasses, and their perspective of selected foraging sites may reflect carrion distribution and condor preferences (Rivers et al. 2014, Hall et al. 2019). Placing carcasses in different vegetation types allowed me to determine condor preference from a known distribution of carrion. I found that, in southern Utah, condors preferentially forage in habitats with less understory cover, indicating a preference for open habitat at foraging sites. This agrees with previous accounts of condors primarily foraging in sparsely vegetated habitats or grasslands (Snyder and Snyder 2000, Rivers et al. 2014, Hall et al. 2019). Understory cover was positively correlated with vegetation height as understory cover ranged from 0 – 2.5 m. As condors have large, unwieldy wings and find carrion using their vision, condors avoid foraging within forests (this study, Rivers et al. 2014). In this study, only one carcass in any forest cover type was visited by condors. Their narrow preference of carcass sites limits the impact of condors on other scavengers by creating refugia for subordinate competitors to forage in. Condors also selected for lower minimum and maximum angles of ascent, as their large wings and weight make steep takeoffs difficult, if not impossible. Similarly, Andean condors will detect carcasses in all terrains, but preferentially forage on carcasses in flatter areas (Perrig et al. 2023). This may be due to safety concerns from approaching mammalian predators and scavengers that defend their carcasses.

Average understory cover was highly correlated with angle of ascent and average canopy, so I could not test these variables independently of each other. Future studies should attempt to disentangle these effects, and observe which are the most important, by targeting carcasses with low understory cover and high average canopy and angles of ascent, and vice versa. Canopy cover may hinder condor discovery of carcasses, while understory cover may impact physical access more. This would have important implications for carcasses shot by hunters, as those carcasses tend to be in forested areas but may not be in especially brushy ones.

Interestingly, distance to public roads did not have a significant impact on condor presence at carcasses, in a logistic model or as a *t*-test. Other large raptors have shown patterns of avoidance of roads depending on distance to road and intensity of vehicle traffic (Bautista et al. 2004, Donázar et al. 2018). In South America, larger raptors, including Andean condors, will avoid scavenging directly on roads (Lambertucci et al. 2009). Condors' willingness to feed on carcasses near roads may be due to the relative low traffic on roads, especially private roads, on Cedar Mountain. Additionally, in this study carcasses were typically placed farther from roads to keep them out of sight of human activity (median distance to any road was >275 m), so the carcasses may not have been close enough to roads to deter condors. The mean distance to public roads was greater for carcasses that I set out (1010 m from road) than for natural mortalities (605 m); when I used a GLMM with only natural mortalities, there was only a small preference for carcasses farther from roads (Appendix A: Table A3). Previous documentation of condors feeding on roadkill near roads exists but is rare, and generally is reported from California. Condors along the California coast may be more habituated to roads and therefore at greater risk of being struck, especially if there is more traffic and the speed limit is higher (Hager 2009). Additionally, the low traffic levels and speed limits on Cedar Mountain limit the amount of wildlife collisions, making condor foraging on roadkill less likely.

Condors selected for carcasses with longer distances to predator cover, showing sensitivity to risk of approaching mammals. There is weak evidence that Andean condors avoid foraging at carcasses closer to predator cover (Perrig et al. 2023). As a long-lived but slow-reproducing species, California condors should be risk averse, especially when there are safe alternative carcasses.

Golden eagles are found across the northern hemisphere and tend to adapt their prey to the local environment, but generally avoid urban or disturbed areas, favoring sagebrush steppes that contribute to orographic lift (Skagen et al. 1991, Marzluff et al. 1997, Domenech et al. 2015). Despite this, eagles have been known to feed on roadkill and suffer mortalities from vehicle collisions (Lonsdorf et al. 2018). My study finding that eagles select for higher understory cover when farther from roads may be a result of impacts of disturbance from humans, as eagles may trade their preferred shrubby habitat (with higher understory cover) for more open areas to be able to take off more easily. Less cover may also mean that eagles can more easily see when cars are coming and monitor the cars' movement across a road. Close to roads, eagles select for similar carcasses as condors do, which may cause increased competition if road networks increase in the study area. Eagles may favor shrubs when roads are not a concern, as it hinders other scavengers and may shade carcasses, slowing the rate of decomposition (Majola et al. 2013, Pardo-Barquín et al. 2019). Other scavengers may avoid shrubby areas where predators could sneak up, but eagles have powerful wings that permit quick takeoffs and can use their strong grasping feet to defend themselves. Indeed, distance to predator cover was not significant for eagles. This may reflect their ability to flee or fight mammalian scavengers if necessary, and golden eagles are known to occasionally defend carcasses from coyotes (Bowen 1980). The eagles' preferred shrubby foraging sites tend to have shorter distances to predator cover, as the vegetation provides cover; if eagles avoided all carcasses with close predator cover, this may severely limit the number of carcasses available to forage on.

Angle of ascent measures how difficult it may be to leave the carcass, either from vegetation or rough terrain. Eagles favored sites with lower minimum angle of ascent, showing a preference for carcasses with at least one direction that is easy to take off from. Large avian scavengers require a large amount of energy to take off, especially if the necessary angle is steep and the bird’s crop is full, which may cause eagles to avoid carcasses with a high minimum angle of ascent. Minimum angle of ascent was correlated with understory cover, so although both were significant in determining eagle presence, I cannot distinguish which may be more important to eagles.

Turkey vultures are known to use carcasses in multiple vegetation communities, but still display unequal foraging across habitats, depending on other scavengers and carrion availability (Coleman et al. 1985, Kirk and Currall 1994, Roen and Yahner 2005). Turkey vultures will readily feed on roadkill and suffer from higher mortality when foraging in areas with greater density of roads (Naveda-Rodríguez et al. 2023). In my study, turkey vultures did not display any avoidance of vegetation characteristics, risk, or disturbance from humans. Turkey vultures may be less sensitive than larger avian scavengers because turkey vultures may be able to take off more easily, ascending faster and without expending as much energy. Subordinate species have been documented to have higher thresholds of acceptable risk and share landscapes with dominant species by using the areas or times the dominant species avoids, especially because of human disturbance (Schuette et al. 2013, Sévêque et al. 2020, Malhotra et al. 2022). Similarly, turkey vultures, as subordinate scavengers, may need to capitalize on any carrion they can find before other scavengers arrive.

Turkey vultures were more likely to visit carcasses earlier in the season than later. There was a smaller amount of carrion available in the pastures early in the summer, before sheep were moved to Cedar Mountain. However, the large scale of avian scavengers' daily movements and varying sources of carrion (roadkill, livestock disease, hunting, and predation) prevented me from quantifying the overall carrion available. The use versus availability of carrion would be an avenue for future research, especially as it impacts other scavengers. This temporal pattern of resource use may also be explained by population changes of turkey vultures. If the last migratory turkey vultures are heading north in early summer, migrating vultures increase competition for carrion, while in the breeding season only resident vultures are present.

Raven habitat use has recently been well-studied, and ravens are considered to use disturbed and fragmented areas, as well as habitat edges, and exploit food provided by human activities and structures (Knight and Kawashima 1993, Webb et al. 2021). I found that ravens were adaptable, as vegetation height did not impact raven use of carcasses. As small and maneuverable avian scavengers, ravens likely face little danger from coyotes or foxes that may find the carcasses. Other habitat covariates could not be tested, as ravens visited few of my carcasses. This may be due to ravens' varied diet, and the availability of alternative food sources, such as seeds and other sources of carrion.

In this study, the data did not indicate that coyotes avoided carcasses closer to public roads. Coyotes change their activity patterns and spatial distribution in response to human activity and infrastructure, and adjust their behavior in response to additional vehicle traffic (Tigas et al. 2002). The relative lack of vehicle traffic at night, when most coyotes arrived at carcasses, may release coyotes from overarching spatial consequences. Previous studies on habitat selection by red foxes have found preference for forest or thickets, likely to avoid dominant coyotes (Gese et al. 1996, White et al. 2006, Van Etten et al. 2007). Based on this, I included coyote presence and average vegetation height as predictors for fox presence. Here, foxes did not avoid carcasses that coyotes visited, and of the 3 carcasses where both species were present, foxes arrived at 2 after coyotes had visited. There was a slight positive effect of vegetation height on fox attendance at carcasses. In Cagnacci et al. (2004), red foxes had no clear pattern of selection during the warm season in an alpine environment, but used high elevations more during the summer than in the winter. Foxes may alter their activity patterns, rather than occupancy, in response to human disturbance, such as roads (Frey and Conover 2006, Baker et al. 2007, Díaz-Ruiz et al. 2016).

Management Implications

Condors in Utah are less likely to attend carcasses with thicker understory cover, so hunted carrion may be more dangerous to condors when in open landscapes, such as grasslands, than in denser areas such as forests. Bedding grounds, where most sheep mortality occurs, often are grazed down and have very little understory cover and longer distances to predator cover. Most sheep mortalities occur on these resting areas, which provides a safe source of accessible carrion for condors. Competition between eagles and condors may be more intense closer to roads than more distant carcasses, as their foraging site preferences overlap. More intense competition can lead to inefficient feeding and increased energetic losses while defending a carcass. Competition may be most intense earlier in the summer, as turkey vultures use carcasses more often and fewer carcasses are available, and avian scavengers may be more likely to use supplemental feeding stations at this time. An increase in human disturbance may increase the competition between eagles and condors and may begin to affect condors, although current levels of road disturbance on Cedar Mountain do not impact condor foraging areas. On Cedar Mountain, roads are scarce, allowing condors to forage on carcasses far from roads. However, increasing the amount of human activity and roads in the future should be discouraged so that condors can continue to use this area safely.

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Tables and Figures

Table 2.1. Means, t-value, degrees of freedom (df), and P-values from *t*-tests for condor, eagle, and vulture presence against habitat variables over summer (May - September) 2022 and 2023, Iron County, UT, USA. Angle of ascent describes the minimum angle required to clear vegetation or topography if taking off from a carcass, measured in 4 cardinal directions. Minimum angle of ascent is the minimum across those 4 directions, and maximum angle of ascent is the maximum measured angle from those 4 directions. Distance to predator cover is the minimum distance at which a 0.5 m^2 board was obscured in any direction.

Scavenger species	Variable	Mean when absent	Mean when present	t-value	df	P-value
Condor	Distance to predator cover	15.58	25.75	-2.77	37.12	0.0088
Condor	Maximum angle of ascent	32.02	14.75	3.73	70.33	0.0004
Condor	Minimum angle of ascent	7.48	0.85	3.90	70.61	0.0002
Eagle	Distance to predator cover	15.56	23.13	-1.89	42.36	0.0663
Eagle	Maximum angle of ascent	29.96	22.92	1.02	39.57	0.3119
Eagle	Minimum angle of ascent	7.57	2.67	2.08	69.93	0.0412
Vulture	Maximum angle of ascent	8.13	6.57	-0.15	62.01	0.8836
Vulture	Minimum angle of ascent	22.92	22.92	0.51	58.56	0.6149

Table 2.2. Parameters in the logistic regression (family=binomial, link=logit) and results testing condor presence against average understory cover and distance to paved road over summer (May - September) 2022 and 2023, Iron County, UT, USA. Average understory describes understory cover from 0 - 2.5m and distance to paved road is the distance between the GPS point of the carcass to the closest public road.

Model:
Condor presence ~ average understory cover + distance to paved road

Fixed Effect	β	Standard Error	P-value
(Intercept)	-0.11	0.64	0.86
Average understory	-1.24	0.52	0.018
Distance paved road	-0.0001	0.0006	0.87

Table 2.3. Parameters in logistic regression (family=binomial, link=logit) and results testing eagle presence against average understory cover, distance to paved road, and an interaction effect between the two variables over summer (May - September) 2022 and 2023, Iron County, UT, USA. Average understory describes understory cover from 0 - 2.5m and distance to paved road is the distance between the GPS point of the carcass to the closest public road.

Model:
Eagle presence ~ average understory cover * distance to paved road

Fixed Effect	β	Standard Error	P-value
(Intercept)	1.42	0.88	0.105
Average understory	-2.89	1.01	0.004
Distance paved road	-0.002	0.0009	0.024
Average profile: Distance paved road	0.002	0.0007	0.0026

Table 2.4. Parameters in the logistic regression (family=binomial, link=logit) and results for vulture presence over summer (May - September) 2022 and 2023, Iron County, UT, USA. Ordinal day established is the ordinal day that the carcass was established, distance to predator cover is the distance between the carcass and the nearest cover that could hide a half-m-squared board, distance to paved road is the distance between the GPS point of the carcass to the closest public road, average vegetation height is the mean of the highest vegetation in a 15m transect from the carcass, and lowest understory is the understory vegetation from 0 - 0.5m.

Model:
Vulture presence ~ ordinal day established + distance to predator cover+ distance to paved road + average vegetation height+ lowest understory

Fixed Effect	β	Standard Error	P-value
(Intercept)	5.23	1.84	0.004
Ordinal day established	-0.024	0.008	0.002
Distance to predator cover	0.003	0.019	0.86
Distance paved road	0.0006	0.0005	0.28
Average vegetation height	-0.0004	0.0009	0.63
Lowest understory	-0.11	0.17	0.50

Table 2.5. Parameters in the logistic regression (family=binomial, link=logit) and results testing raven presence against average vegetation height over summer (May - September) 2022 and 2023, Iron County, UT, USA. Average vegetation height is the mean of the highest vegetation in a 15 m transect from the carcass.

Model:
Raven presence ~ average vegetation height

Fixed Effect	β	Standard Error	P-value
(Intercept)	-1.47	0.35	2.26E-05
Average vegetation height	-0.001	0.002	0.45

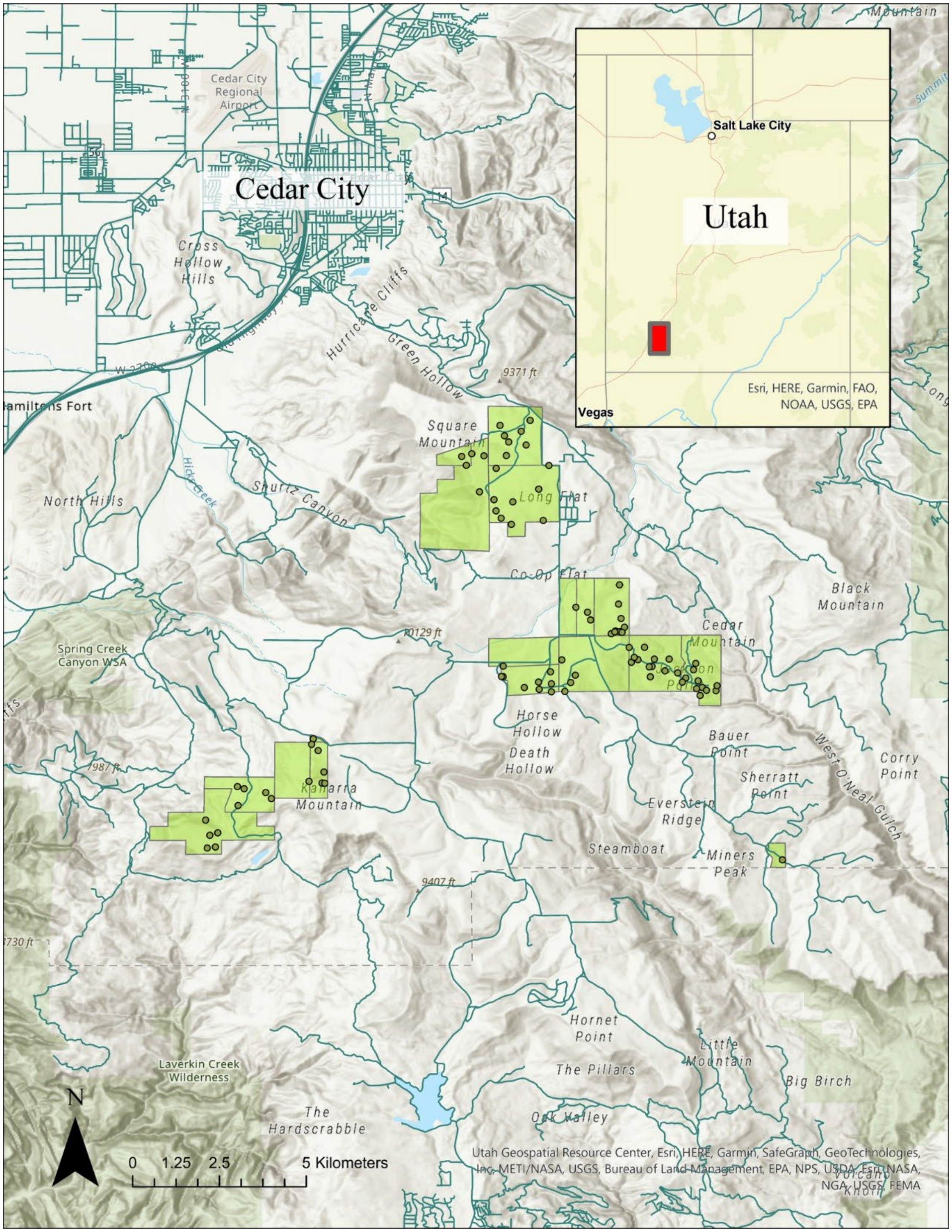
Table 2.6. Parameters in logistic regression (family=binomial, link=logit) and results testing coyote presence against distance to paved road over summer (May - September) 2022 and 2023, Iron County, UT, USA. Distance to paved road is the distance between the GPS point of the carcass to the closest public road.

Model: Coyote presence ~ distance to paved road			
Fixed Effect	β	Standard Error	P-value
(Intercept)	-1.55	0.65	0.017
Distance paved road	-6.85E-05	0.0006	0.91

Table 2.7. Parameters in the logistic regression (family=binomial, link=logit) and results testing fox presence against average vegetation height and coyote presence over summer (May - September) 2022 and 2023, Iron County, UT, USA. Average vegetation height is the mean of the highest vegetation in a 15m transect from the carcass and coyote visit is a binary indicator of coyote presence at the carcass.

Model:
Fox presence ~ average vegetation height + coyote visit

Fixed Effect	β	Standard Error	P-value
(Intercept)	-0.84	0.32	0.008
Average vegetation height	0.0014	0.0009	0.11
Coyote visit	-0.17	0.74	0.82



Esri, HERE, Garmin, FAO, NOAA, USGS, EPA

Utah Geospatial Resource Center, Esri, HERE, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, USDA, Esri, NASA, NGA, USGS, FEMA

Figure 2.1. Location of study site in southern Utah, USA, May - September 2022, 2023. Carcass locations are indicated within private pastures, which are denoted in green.

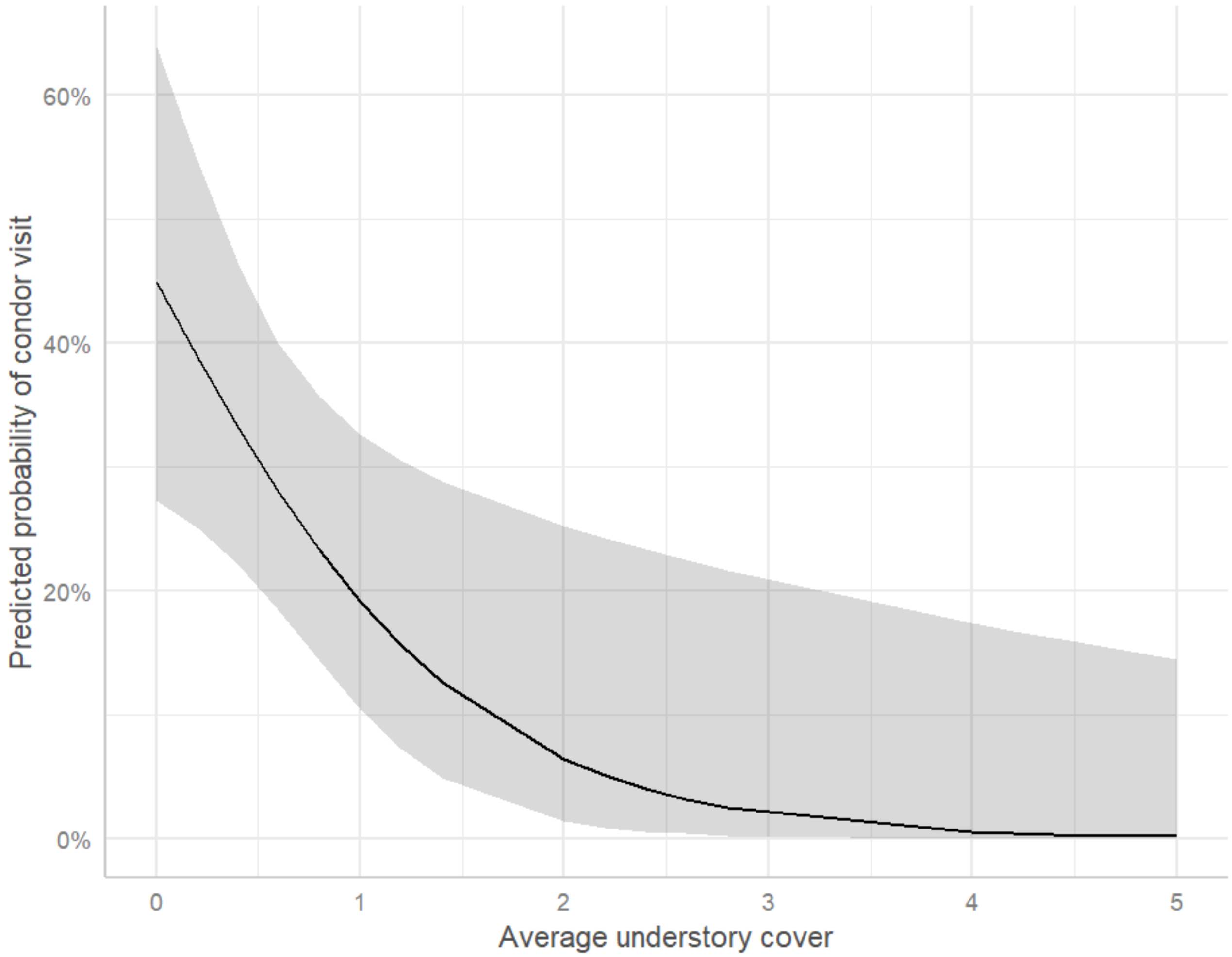


Figure 2.2. Results of the logistic regression, indicating the influence of understory cover on predicated probability of a condor visiting a site, Cedar Mountain, Utah, May - September 2022, 2023.

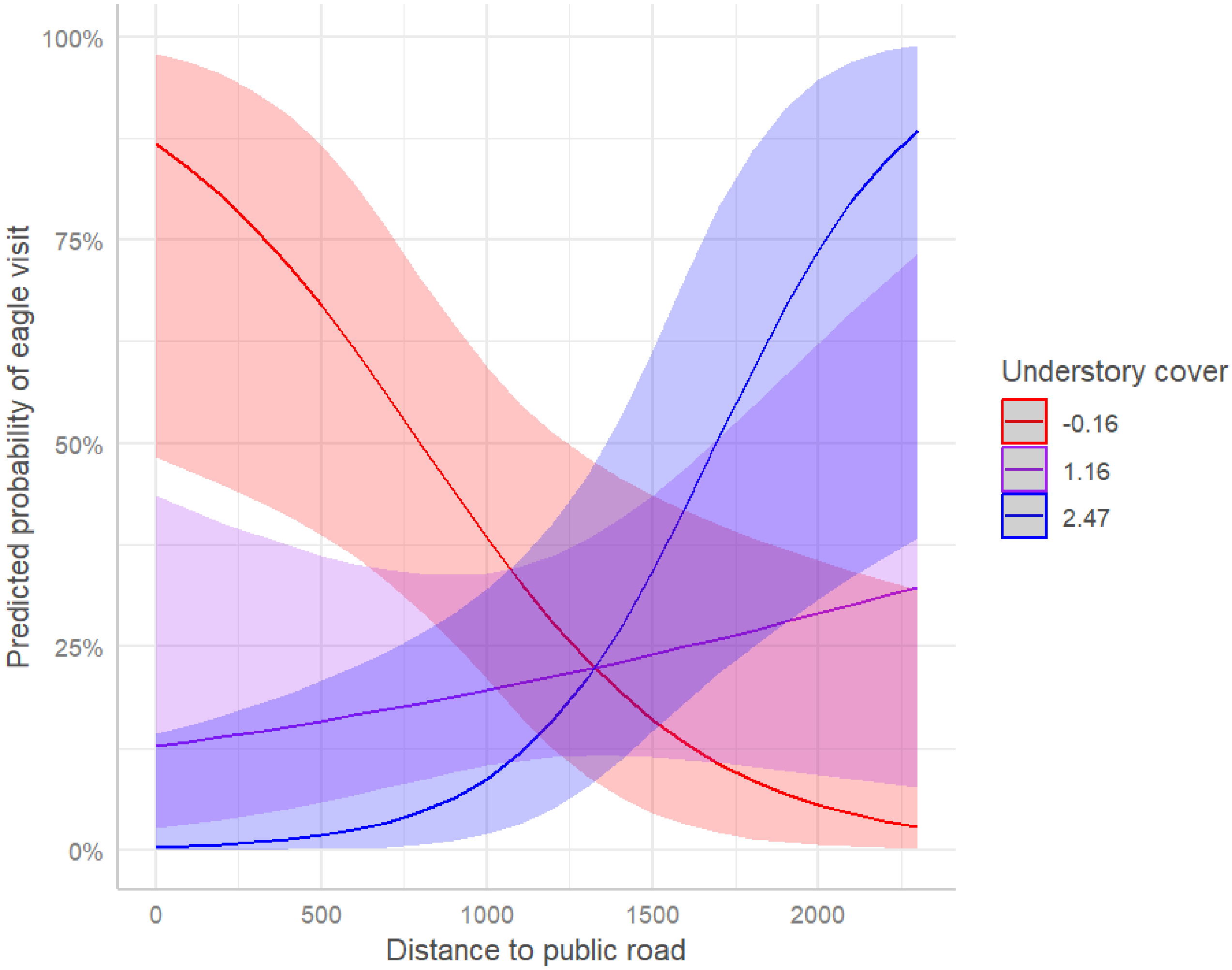


Figure 2.3. Results of the logistic regression indicating the interaction effect between 'distance to road' and understory cover on the probability of an eagle visiting a carcass, Cedar Mountain, Utah, May - September 2022, 2023.

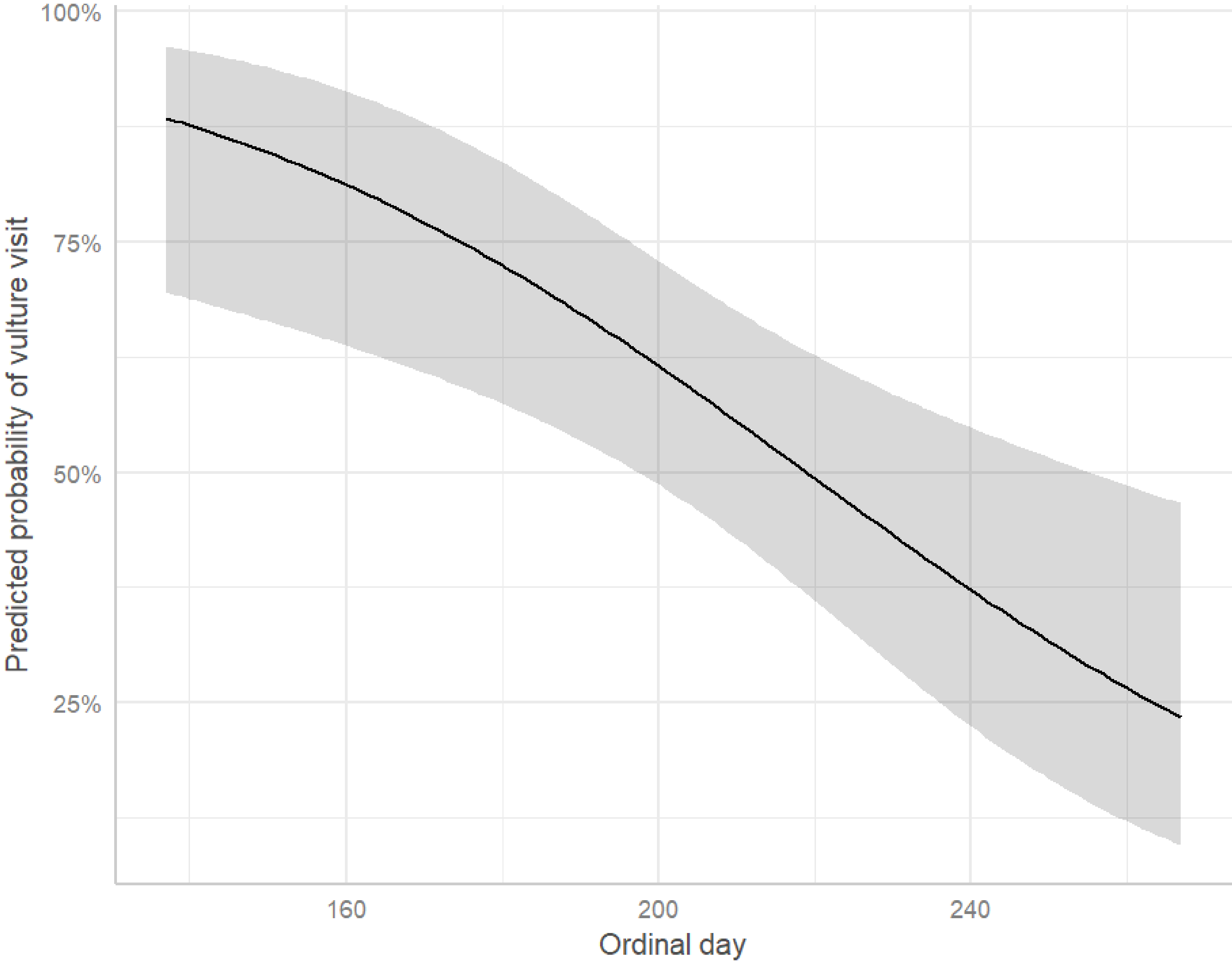


Figure 2.4. Results of the logistic regression, indicating the influence of ordinal date on predicated probability of a vulture visiting a site, Cedar Mountain, Utah, May - September 2022, 2023.

CHAPTER III

CALIFORNIA CONDORS, GOLDEN EAGLES, AND TURKEY VULTURES EXHIBIT FLEXIBLE VIGILANCE ACROSS FORAGING SITES

Abstract

The ability of scavengers to accurately perceive the riskiness of a carcass site and modify their behavior accordingly is crucial to safely feeding on carrion. Especially for avian scavengers, carrion is a risky food source, as predators defend their kills and mesocarnivores are attracted to carcasses. Vigilance is one strategy to detect approaching competitors that are potentially dangerous, but there is a trade-off; spending time vigilant makes feeding less efficient and increases the total amount of time spent at a carcass. Changing the proportion of time spent vigilant across foraging habitats allows scavengers to match their behavior to perceived riskiness to maximize safety and caloric intakes. To study this trade off in avian scavengers, I set up camera stations on 76 naturally occurring and staged carcasses May - September 2022 and 2023. Using generalized linear mixed models, I assessed vegetative, disturbance, and climate variables that might impact the proportion of time California condors (*Gymnogyps californianus*), golden eagles (*Aquila chrysaetos*), and turkey vultures (*Cathartes aura*) spent vigilant while visiting a carcass. The top model determined condor vigilance positively influenced by wind speed and temperature. Other models showed significant impacts of group dynamics though the number of other individuals present at a carcass and the number of displacements caused by the focal individual, as well as safety of carcasses through slope and distance to predator cover. Eagle vigilance was positively correlated with foraging-group size of any species and negatively correlated with number of displacements of other scavengers

caused by the focal eagle. The presence of condors at carcasses can force eagles to be less efficient when feeding, especially because condors arrive in groups. Turkey vulture vigilance was negatively correlated with carrion biomass remaining upon arrival. Turkey vultures may be prioritizing feeding over vigilance when arriving at large, intact carcasses that are likely to be monopolized by condors. Avian scavengers modified their behavior based on different cues, which suggests different yet successful strategies for balancing energetic demands and safety, and potentially different perceptions of risk at foraging sites.

Introduction

The ability of scavengers to accurately determine the riskiness of a carcass site and modify their behavior accordingly is crucial to safely feeding on carrion. In southern Utah, potential avian scavengers at carcasses include California condors (*Gymnogyps californianus*), golden eagles (*Aquila chrysaetos*), turkey vultures (*Cathartes aura*), and common ravens (*Corvus corax*). Animals tend to die in areas that may also be dangerous for scavengers, for example, denser habitat with little escape terrain or on roads, and scavengers feed on carcasses that may be visited by other predators and scavengers (Perrig et al. 2023). There is a trade-off between feeding and risk avoidance, which is especially pertinent to condors due to their difficulty in taking off. In addition, the amount of time spent feeding and traveling can impact breeding success of vultures (Fluhr et al. 2021). Populations of scavengers may decline if costs associated with behavioral changes, such as inefficient feeding due to increased vigilance, cannot be sufficiently minimized across available carrion.

Carrion is a risky food source for avian scavengers, as predators defend their kills and mesocarnivores are attracted to carcasses. Mountain lions (*Puma concolor*) are known to kill competitors when defending kills (Koehler and Hornocker 1991); between 1992 and 2020, 28 California condors have been killed by predators, including by coyotes (Woods and Heinrich 2007, U.S. Department of the Interior 2020). One way to counteract the riskiness of foraging sites is to increase vigilance if the perceived danger is high. Coyotes (*Canis latrans*) are more vigilant when feeding at carcasses in areas with greater wolf (*Canis lupus*) activity (Switalski 2003) and will seek to avoid apex predators while continuing to consume their kills (Ruprecht et al. 2021). Andean condor (*Vultur gryphus*) vigilance decreases when the carcass is farther away from cover that would hide an approaching predator (Perrig et al. 2023). For example, ravens, common buzzards (*Buteo buteo*), and white-tailed eagles (*Haliaeetus albicilla*) are more common at carcasses in open areas, possibly due to ease of detection and access, but so are domestic dogs (*Canis lupus*; Selva et al. 2005). Vegetation can obscure approaching scavengers and predators or make takeoff more difficult. Coyotes are more vigilant at wolf kills with greater lateral obstruction, which can hinder escape routes and act as cover for approaching wolves (Atwood and Gese 2008). Turkey vultures are more common in wooded habitats than in edge or open areas, but they are also more vigilant in wooded habitats, possibly due to thicker understory and limited visibility (Roen and Yahner 2005). However, this pattern does not hold true for all avian scavengers; black vultures (*Coragyps atratus*) select for wooded areas but are most vigilant in edge habitat, and American crows (*Corvus brachyrhynchos*) are more common in edge and open areas but most vigilant in edges and woods (Roen and Yahner 2005). I expected vultures to be more vigilant in habitat closer to predator cover, when competing with more individuals, and with greater human disturbance. I hypothesized that eagles may be more vigilant at carcasses with more competitive pressure and with greater human disturbance. I expect lower vigilance in open habitat in condors, as their large wingspan and heavy weight makes takeoff difficult, which may be compounded by taller vegetation, leaving condors without an accessible way to retreat from perceived danger.

Current scavenger activity can impact how an individual behaves during its visit to a carcass. For example, vigilance in Andean and California condors decreases with increased conspecific group size (West 2009, Perrig et al. 2023). Similarly, turkey vultures will decrease their vigilance with increased group size, with varying interactive effects of predation risk (Clark-Phinney 2001, Beauchamp 2019). Conversely, golden eagles in larger conspecific groups increase their vigilance, contrary to passerines, as intraspecific thievery and attacks are the primary concern rather than predation risk (Knight and Knight 1986). Effects of increased mixed-species group size is unknown for most avian scavengers.

Human disturbance can impact avian scavengers' behavior differently depending on the species (Skagen et al. 1991). Traffic creates carcasses but can also be risky to scavengers profiting from roadkill, and scavengers may perceive approaching vehicles as dangerous. Andean condors are more vigilant at carcasses closer to roads (Speziale et al. 2008). Other raptors will avoid roads only when traffic levels increase (Bautista et al. 2004). Although some vultures regularly feed on roadkill, condors typically avoid feeding on carcasses directly on roads (U.S. Department of the Interior 1996). Turkey vultures and coyotes use carcasses equally across roads, forest, and power-line clearings, which could signify resilience to human disturbance (Hill et al. 2018).

Energy budgets and foraging strategies vary among scavengers in response to changes in weather (Fluhr et al. 2021). As temperatures decline, caloric need, and therefore scavenging, increase (Selva et al. 2005). Competition for carrion is stronger among avian scavengers in the winter, when carrion availability is typically low (Blázquez et al. 2009). However, during the summer, California condors decrease their vigilance as temperatures rise, potentially because higher temperatures coincide with decreased mammalian activity in the middle of the day (West 2009).

Few studies have examined the effect of carcass weight on scavenger behavior, although carcass size and state of decomposition shape the scavenger community attracted to the carcass (Turner et al. 2017). Ubiquitous scavengers, such as turkey vultures, may alter their behavior based on carcass size, as smaller carcasses may be more readily defended and consumed in one sitting. Eagles may also carry away carcasses that are small enough to be moved to a safer area (Moreno-Opo et al. 2016).

Habitat use of scavengers reflects a balance of food availability and safety (Lambertucci et al. 2009). However, even if scavengers are still willing to feed on a carcass in suboptimal areas, they may display a preference for safer feeding areas by being less vigilant, increasing visit duration, or eating a greater proportion of safer carcasses. There is a paucity of research on flexibility of behavior in avian scavengers. In this study, I study scavenger foraging patterns in southern Utah, namely Cedar Mountain and the surrounding area, to examine how foraging-site characteristics, human disturbance, competition, weather, and carcass weight shape their behavior at carcasses. I hypothesize that complex vegetation, closer predator cover, greater numbers of competitors, increased human disturbance, colder weather, and larger carcasses lead to increased vigilance and less efficient feeding in condors, eagles, and vultures, and I test which variables are most important to vigilance in each species.

Methods

Study area

Cedar Mountain is a primarily privately owned plateau 2600 m above sea level and used as summer pastures for sheep (*Ovis aries*) in Iron County, Utah. To monitor scavenger activity, I placed trail cameras at naturally occurring sheep mortalities and previously collected stillborn lambs on 1900 ha, owned by 7 different landowners (Fig. 3.1). Vegetative communities were predominantly grassland and aspen (*Populus tremuloides*) forests, with less frequent shrublands (principally *Artemisia tridentata*) and aspen-conifer or coniferous forest (*Abies lasiocarpa and Pseudotsuga menziesii*; Rogers et al. 2010).

Study design

My field season started in May during 2022 and June during 2023, when the snow had thawed enough to access Cedar Mountain, and continued through September of each year. California condors arrive on Cedar Mountain in mid-June and remain until October, coinciding with the arrival of sheep on the mountain (Palmer 2009). In summer 2023, the Arizona-Utah population of condors included 95 individuals, all from one release site in Vermilion Cliffs, Arizona. Every fall since 1996, more condors are released at Vermilion cliffs, 80 km away. Scavengers on Cedar Mountain include mountain lions, black bears (*Ursus americanus*), red foxes, coyotes, striped skunks (*Mephitis mephitis*), condors, turkey vultures, golden eagles, and common ravens. Scavenger populations across the summer months are relatively stable, as vulture migration has concluded and only 12 permits for black bear are available across the hunting unit that encompasses Cedar Mountain and the surrounding area (Utah Division of Wildlife Resources 2024).

At the beginning of each field season, I consulted with sheep producers and confirmed where the sheep bedding grounds were on each pasture, as depredation most commonly occurs at twilight, when sheep are on or near the bedding grounds. I systematically searched for sheep mortalities on pastures, walking along sheep trails from bedding areas to resting areas (similar to Palmer et al. 2010), and investigated any reports of mortalities from ranchers and shepherds. As I found fewer carcasses than expected during the summer, I searched for mule deer (*Odocoileus hemionus*) carcasses while driving over Utah State Route 14 on the approximately 60 km between Cedar City and Duck Creek Village, Utah, as well as obtaining locations of roadkill from Utah Division of Wildlife Resources in 2022. To supplement the sample size of naturally occurring carcasses, in 2022 I distributed ewe and lamb carcasses obtained from ranchers within the study area. In 2023, I obtained and froze lamb carcasses from sheep producers during spring lambing (April-May) in anticipation of summer fieldwork, and primarily relied on setting out lamb carcasses rather than expanding efforts to search for mortalities in pastures. I tried to hide my scent by minimizing time at a site and handling all carcasses with gloves.

While many ewe carcasses were used ‘in situ’, I also moved carcasses found on Cedar Mountain to pre-determined sites, similar to the placement of supplemental carcasses. To determine where to place supplemental carcasses, I used ArcGIS (ESRI

2023) to view pastures where I had landowner permission to access. I used stratified random sampling within accessible areas, defined as slope <45°, within 5 km of a road, and >100 m from any buildings, to randomly generate an equal number of points across vegetation types. Points also had to be farther than 200 m from each other, to capture the variety in vegetation types and avoid scavengers learning carcass sites. I downloaded the layer of existing vegetation types from the Landscape Fire and Resource Management Planning Tools Project (LANDFIRE 2020) and combined vegetation types into 10 categories including deciduous forest, evergreen forest, savanna, grassland, sparse vegetation, shrubland, modified land, wetland/riparian, agriculture, and unsuitable habitat (e.g., open water). This classification method is similar to those used in Stoms et al. (1993) and Rivers et al. (2014) for condor space use. I placed carcasses farther than 2 km from the nearest simultaneously active carcass to avoid overlap in detection by scavengers based on proximity (similar to Speziale et al. 2008). In 2022, when I found roadkill on the state highway, I collected it and relocated it as soon as possible to the next potential location on Cedar Mountain. Roadkill was only used if it was fresh, in good condition, and <70 kg. Every week over the summer of 2023, in addition to locating naturally occurring sheep carcasses, I set out at least 2 carcasses, each consisting of one or more frozen lambs (total initial weight 3 - 20 kg).

I used trail cameras (Campark T20 Mini Trail Camera, Campark Electronics, Portland, OR) placed on trees, fence posts, or staked metal poles, approximately 1 m off the ground to record visits from scavengers. I scheduled cameras to take 30-s videos with 5-s intervals whenever motion was detected, with low sensitivity to minimize videos of vegetation moving with wind. I used 16 GB to 64 GB SD cards (SanDisk, Milpitas, CA).

I placed 2 cameras on each carcass, one ~3 m away and one ~5 m away, at 90° from each other, to avoid missed scavenger visits from size differences, scavengers dragging carcasses in different directions, and camera failure. I tied a cable snare around the neck of each carcass and staked the cable into the ground with 45-cm-long steel stakes to prevent the carcass from being dragged out of the cameras' frame.

I checked camera batteries and SD cards at least weekly and replaced these as needed. Trail cameras were continuously active at carcasses until carcasses were at least 75% consumed, had been out for at least a week, or reached such an advanced stage of decay that most mammalian and avian scavengers would not feed on the carcass due to putrefaction. I calculated the proportion of the carcass consumed by visual estimation during these checks, serving as known reference points compared to video estimation of carcass consumption.

Effects of habitat

When placing the carcass, I measured several potentially explanatory landscape variables. I chose a random compass direction by spinning a compass dial and used the resulting bearing to create a 15 m transect. I measured understory density by placing a Nudd's profile board (Nudd 1977) with 5 stacked 0.5-meter-high sections at the 15-m end of the transect, read from the beginning of the transect. Each section was given a score from 0 to 5, representing the percent of the board covered by vegetation along the transect. To measure dominant vegetation height, I recorded the tallest vegetation that intersected every meter along the transect, starting at the carcass. I then calculated the average vegetation height for each 15-m transect. Additionally, I calculated slope using the clinometer on a compass (Silva Ranger 2.0 compass, Silva, Sandy, UT, USA).

I digitally calculated distance from each carcass to the closest trafficked and public roads using ArcGIS. I defined trafficked roads as maintained dirt/gravel roads that were used by someone at least weekly, signifying active human disturbance. I defined public roads as those that were used several times each day and were paved or well-maintained dirt roads that had public access. Road layers were downloaded in November 2023 from ArcGIS Hub's Utah Roads dataset, compiled by the Utah Automated Geographic Reference Center. The "local roads" layer included private roads and was used as my trafficked roads, and I removed roads known to be private and only accessible through locked fences to create a public roads dataset. The closest distance to both types of roads were automatically calculated from GPS points of carcasses using the 'near_dist' function in ArcGIS.

Using a tape measure, I calculated distance to predator cover. Distance to predator cover was the closest distance in any direction at which a half meter-squared checkerboard could be completely hidden by thick vegetation or terrain. This imitates the size of a coyote approaching head-on, to gauge the risk of a mammalian predator approaching unseen. If there was no cover that would conceal the board within 50 m, I recorded distance as 50 m.

Recording scavenging behavior from videos

At the start of every scavenger visit, I recorded time, weather, species and number of other individuals (combined across all species present), and proportion of the carcass that was eaten. Time was displayed on the video from the camera. Weather included wind, visually estimated using the Beaufort scale (National Weather Service 2022), cloud cover, visually estimated as a percentage, and the camera's reported temperature. I also created a visit number that ascended with each visit from any scavenger per carcass. When the scavenger left, I recorded the time, species and number of other individuals, and approximate proportion of the carcass consumed. The maximum number of other individuals across arrival and leaving from each visit was used as maximum group size. Arrival weight was calculated from the percent eaten at arrival and initial weight when the carcass was established.

Visits were defined as any scavenger in the camera's frame for any length of time, regardless of feeding activities. If a scavenger left the frame and was not seen for >15 minutes afterwards, the visit was ended when the scavenger exited from view, and subsequent reentry in frame was counted as a new visit. When individuals had unique tags (i.e. condor wing tags or dog collars), their identity was also recorded. Individuals that were not identifiable were kept track of through location and general movement, as the time lapse between videos was a minimum of 5 seconds.

I created an ethogram within Behavioral Observation Research Interactive Software (BORIS, Friard & Gamba, 2016) to efficiently record behavior from the collected videos. For each visit by any scavenger, I recorded feeding, vigilance, and other behaviors (including moving, preening, and aggression). These data were summed individually to create time of feeding, vigilance, and other behaviors, respectively. I also summed them together as time of known behavior. Feeding was defined as head down with the beak touching the carcass. Vigilance was defined as having the head raised without the bird moving. Additionally, the time of behavior that could not be determined, such as if the individual was out of frame for a short time or too far away to confidently categorize, was recorded as unknown and was added to the time of known behavior to create summed time of all behaviors. Displacements, defined as one individual leaving due to aggressive actions by another, were also recorded, and total displacements were summed for each visit. Displacements of the same individual multiple times during one visit were counted as separate instances.

Data analysis

All statistical analyses were conducted in R (version 4.2.1, R Core Team 2021) with package "tidyverse" (version 1.3.2, Wickham et al. 2019). Statistical difference was determined at $p = 0.05$. Vigilance and feeding were negatively correlated ($r = -0.83$) so only vigilance proportion was used as a response variable. For a visit to be included in the analysis, the summed time of all known behaviors had to be > 60 seconds. I created 6 generalized linear mixed models (GLMMs) using a logit link and beta distribution (Table 3.1). Each model represented an a priori hypothesis with the proportion of time spent vigilant as a response variable. Finally, I also included a null model with no fixed effects, only keeping the random effects. All 7 models had carcass number and the visit number for the carcass as random effects. The weather model was only included for condors, as temperature was missing for some visits of eagles and vultures. All covariates were tested for correlation prior to running models, and no correlated variables, defined as $|r| > 0.6$, were used jointly in a model. The proportion of behaviors was weighted using the time of all behaviors, using the 'glmmTMB' package (version 1.1.8, Brooks et al. 2017). Aikeke's Information Criterion (AIC, Akaike 1987) was used to select the most competitive models, considering all models with an AICc of <8. I modeled vigilance based on each priori hypotheses for vultures, condors, and eagles separately, as different avian scavengers may be influenced by different sets of variables. I used an analysis of variance (ANOVA) and post-hoc Tukey test to test differences in the proportion of vigilance across species.

Results

In 2022, 39 carcasses were monitored, and in 2023, 50 carcasses were included. Of those, 83 were fresh enough to deploy cameras. However, several cameras failed, resulting in video for 76 carcasses. Of those, 81% had videos of scavengers. I initially had 772 recorded visits of scavengers, and after removing all observations that had <60 seconds of known behaviors (including feeding, vigilance, and other), the dataset included 458 visits. When comparing species to each other, the proportions of time spent vigilant by condors and eagles were significantly different from that of vultures (Appendix B: Table B1). Mean proportion of time spent vigilant was greater for vultures ($\bar{x} = 0.50$, SD = 0.17) than for condors ($\bar{x} = 0.40$, SD = 0.18, $p = 0.005$) and eagles ($\bar{x} = 0.40$, SD = 0.20, $p < 0.001$, Table 3.2). Condors spent the greatest amount of time vigilant, followed by vultures and eagles (Table 3.2).

The top model for condors, determined through AIC, was the weather model (Table 3.3). Effects of both wind speed ($p < 0.001$) and temperature ($p < 0.001$) were significant and positively correlated to condor vigilance (Table 3.4). Increasing the wind speed by one unit on the Beauford scale led to a 62% increase in the odds of proportion of time that condors were vigilant. Increasing the temperature by 1° C increased the odds of proportion of time vigilant by 34% (Fig. 3.2). No other models were competitive. Non-competitive models did show significant effects of maximum group size, number of displacements caused, and an interaction between distance to predator cover and slope

(Appendix B: Table B2). Condors were more vigilant with larger group sizes, less vigilant with larger numbers of displacements caused, at steep slopes close to predator cover, and at low slopes far from predator cover. Across models, average vegetation height, understory cover, distance to paved and any roads, arrival weight, and date of carcass establishment were tested and did not have a significant impact on condor vigilance.

The only competitive model for vultures was the carcass model (Table 3.5), including a significant effect of the carcass weight ($p < 0.001$, Table 3.6). For every additional kg of carcass remaining when the vulture arrived, the odds of proportion of time spent vigilant decreased by 4% (Fig. 3.3).

The top model for eagles was the competition model (Table 3.7). Effects of both maximum number of scavengers of all species and number of displacements caused by the focal individual were significant with $p < 0.001$ (Table 3.8). For every additional individual present at arrival or departure, the odds of eagle proportion of time spent vigilant increased by 22%. For every additional displacement caused, the odds of eagle vigilance proportion decreased by 33% (Fig. 3.4).

Discussion

Previous research shows that vultures are more vigilant in woodlands compared to more open and edge habitats in the eastern U.S. (Roen and Yahner 2005), but this pattern may not extend to other areas with different available habitats, competitors, and distribution of carrion, and may not be applicable to other avian scavenger species. I expected different influences of vigilance among the three scavengers. Condor behavior has only been studied at established feeding stations that are regularly used, with little variation in habitat and potential for condor acclimation to feeding sites (West 2009). Sites with predictable resources, such as these stations, tend to favor larger, more dominant scavengers (Cortés-Avizanda et al., 2010, Cortés-Avizanda et al., 2012).

The proportion of time spent vigilant was significantly higher for vultures than for eagles and condors. In my study, vultures visited carcasses in all vegetation types, with variable potential danger, while condors selected more open areas with greater visibility, which may warrant less vigilance. Of these 3 species, vultures are the smallest and likely least dominant, and so may have to stay vigilant for other avian scavengers in addition to mammalian carnivores.

Wind speed was positively correlated with condor vigilance. This contrasted with other studies on condor vigilance, where wind speed was measured but not present in the top model. As a k-selected species, condors may prioritize safety over food acquisition, and increase their vigilance when there is more wind. Higher wind speeds move ground vegetation, which may be perceived as threats or obscure them. Wind speed may also make takeoff in certain directions impossible, increasing the risk if a predator approaches from the opposite direction and the individual can only escape by flying into the wind.

In southern Utah, condor vigilance increased with temperature; in contrast, a prior study on condor vigilance reported a negative relationship with temperature, possibly due to lower temperatures correlating with times of day when potentially dangerous scavengers are most active (West 2009). West (2009) observed condor behavior at established feeding stations, which may attract mammalian scavengers and predators as a long-standing food source. Additionally, predators in my study were rarely observed, and foxes and coyotes most often visited at night, when condors were not active. Alternately, metabolic pressures can lead to increased feeding at low temperatures (Selva et al. 2005). Although this study was conducted over the summer, temperatures varied both across the season and during the day, and metabolic needs may have played a role in this result.

Condors were more vigilant with larger group sizes. This contrasts with Andean condors, which have higher foraging rates and lower percent of individuals vigilant as group size increases (Perrig et al. 2023). California condors may experience higher intraspecific aggression rather than potential attacks from scavengers approaching the carcass. California condors may have a stricter dominance hierarchy, where subordinate individuals are not able to feed when dominant individuals have control of a carcass, and any non-dominant individuals are vigilant while waiting their turn. This would agree with the observation during this study that individuals that caused more displacements were less vigilant. These individuals were probably dominant and had a higher proportion of time spent feeding. The coefficient on the interaction between distance to predator cover and slope was very small, but indicates that condors require either a flat area, where it is easy to take off in any direction, or a long distance to predator cover to exhibit low vigilance.

Vultures' low aspect wings and low wing loading allow them to take advantage of weaker thermals but make takeoff slow (Graves 2017), and individuals should minimize their time on the ground to stay safe. However, individuals need to feed, and vultures do not have grasping talons to move carrion to safer locations. Vultures were less vigilant when there was more carrion available. This was unexpected as larger carcasses bring in more scavengers and may therefore be riskier (Buckley 1996, Perrig et al. 2023). If large amounts of carrion are more likely to attract other animals that are themselves likely to displace vultures, the most beneficial strategy for vultures may be to spend as much time possible foraging, which would necessitate decreasing the amount of time spent vigilant. Turkey vultures do not preferentially feed in groups (Estrella 1994) and may be overwhelmed by groups of other scavengers (Buckley 1997). In contrast, the foraging rate decreases for Andean condors, which are dominant scavengers, when there is more carrion remaining (Perrig et al. 2023). This pattern holds true in other instances where the scavenger is not the dominant species. Hyaenas (*Crocuta crocuta*) are less vigilant and more focused on feeding at higher-quality carcasses, which were likely to attract more dominant scavengers (Pangle and Holekamp 2010). Similarly, coyotes increased their vigilance at carcasses after wolves were reintroduced into Yellowstone National Park (Switalski 2003).

While there is not much data regarding golden eagle foraging vigilance, research suggests that bald eagles (*Haliaeetus leucocephalus*) in large groups (>8 individuals) have higher vigilance than those in smaller groups, as defense against conspecific attacks became more important than defense against predators or humans (Knight and Knight 1986). The proportion of time spent vigilant among golden eagles during my study also increased with group size of eagles, although group size only ranged from 1 to 8 individuals. Additionally, the proportion of time a focal individual spent vigilant decreased as the number of displaced conspecifics increased. Aggressive individuals may spend less time vigilant because they are spending time moving around the carcass and acting aggressively towards conspecifics.

The primary aim of this study was to determine what variables, if any, contribute to allocation of time to vigilance across species. All avian scavengers modified their behavior based on different environmental variables, which suggests different yet successful strategies for balancing energetic demands and safety across the avian scavenger guild. Interestingly, the top model for condors did not directly indicate an impact of predation risk or competition with other scavengers. Condor’s large size and ability to intimidate other species may allow condors to maintain the same vigilance across carcasses. Dominant avian scavengers may display behavioral shifts that are more similar to dominant mammalian scavengers than other avian scavengers, and future research is warranted on the plasticity of scavenger behavior across carcasses and how behavior can affect breeding success. This is especially important for species of conservation concern in Utah, including condors and eagles.

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Tables and Figures

Table 3.1. Explanatory variables included in the 7 generalized linear models tested for each species. Each model was evaluated separately for its accuracy describing vigilance changes observed in condors, golden eagles, and vultures; Cedar Mountain, Utah, 2022-2023. All models had carcass number and visit number as random effects. Distance to predator cover is the distance between the carcass and the nearest cover that could hide a half-m-squared board and slope is the slope taken at the carcass site. Average vegetation height is the mean of the highest vegetation in a 15m transect from the carcass, and understory cover is the understory vegetation measured from 0 – 0.5 m. Distance to paved road and distance to all road is the distance between the GPS point of the carcass to the closest public road and closest road (including dirt roads), respectively. Maximum group size is the maximum of group sizes taken at focal individual arrival and departure. Number of displacements is the sum of all displacements caused by the focal individual. Date of carcass establishment is the ordinal day that the carcass was established, and carcass weight at arrival was the measured initial carcass weight multiplied by visually estimated percent of carcass remaining at focal individual arrival. Wind speed was visually estimated over video, and temperature was recorded by the trail cameras.

Model	Variables for fixed effects
Predator	Distance to predator cover * slope
Vegetation	Average vegetation height + understory cover
Human disturbance	Distance to paved road + distance to all road
Competition	Maximum group size + number of displacements
Carcass	Date of carcass establishment + carcass weight at arrival
Weather	Wind speed + temperature
Null	.

Table 3.2. Median time spent vigilant across species, Iron County Utah, May-Sept 2022, 2023.

Species	Vigilance time (s)
Condor	277.35
Vulture	169.72
Eagle	126.31
Great horned owl	91.90
Raven	85.13
Domestic dog	68.08
Fox	53.73
Coyote	17.36
Skunk	8.97

Table 3.3. Degrees of freedom, Akaike Information Criterion (AIC), and delta AIC for all generalized linear mixed models tested on proportion of time spent vigilant by condors, Iron County, Utah, May - September 2022, 2023. Each model contained random effects of carcass number and scavenger visit number. All but the null model tested two explanatory variables.

Model	Df	AIC	delta AIC
Weather	6	-124858	0
Competition	6	-121707	3151
Predator	7	-117348	7510
Null	4	-117344	7514
Carcass	6	-117344	7514
Vegetation	6	-117342	7516
Human disturbance	6	-117340	7518

Table 3.4. Estimates, standard error, Z value, and p value from the top GLMM for condor vigilance in Iron County, Utah, May - September 2022, 2023.

	Estimate	SE	Z	Pr (>|z|)
(Intercept)	-8.94	0.65	-13.69	1.10e-42
Wind	0.49	0.01	42.88	0
Temp	0.29	0.003	88.35	0

Table 3.5. Degrees of freedom, Akaike Information Criterion (AIC), and delta AIC for all models tested on vulture proportion of time spent vigilant, Iron County, Utah, May - September 2022, 2023.

Model	df	AIC	delta AIC
Carcass	6	-235394	0
Competition	6	-234610	784
Human disturbance	6	-230558	4836
Predator	7	-230555	4839
Vegetation	6	-230555	4839
Null	4	-227448	7946

Table 3.6. Results from the top GLMM model for vulture vigilance in Iron County, Utah, May - September 2022, 2023.

	Estimate	SE	Z	Pr (>|z|)
(Intercept)	1.78	2.20	0.81	0.42
Arrival weight	-0.04	0.0006	-70.42	0
Ordinal day established	-0.005	0.01	-0.47	0.64

Table 3.7. Degrees of freedom (df), Akaike Information Criterion (AIC), and delta AIC for all models tested on eagle proportion of time spent vigilant, Iron County, Utah, May - September 2022, 2023.

Model	df	AIC	delta AIC
Competition	6	-107314	0
Carcass	6	-89764	17550
Null	4	-89506	17808
Predator	7	-89503	17811
Vegetation	6	-89503	17811
Human disturbance	6	-89502	17812

Table 3.8. Results from the top GLMM model for eagle vigilance in Iron County, Utah, May - September 2022, 2023.

	Estimate	SE	Z	Pr (>|z|)
(Intercept)	-0.49	0.21	-2.32	0.02
Max group	0.20	0.003	69.20	0
Number of displacements	-1.09	0.008	-140.37	0

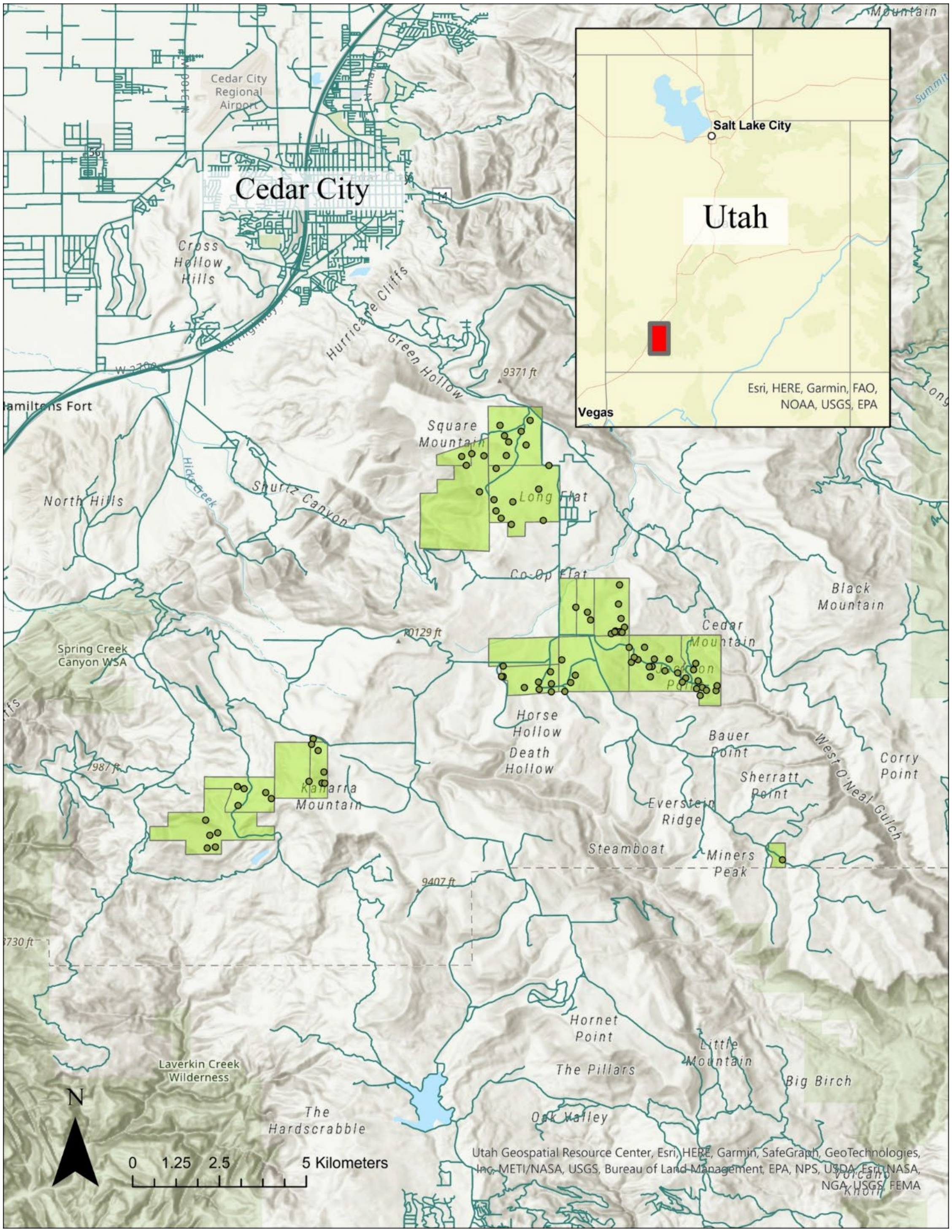

Figure 3.1. Location of study site in southern Utah, USA, May - September 2022, 2023. Carcass locations are indicated within private pastures, which are denoted in green.

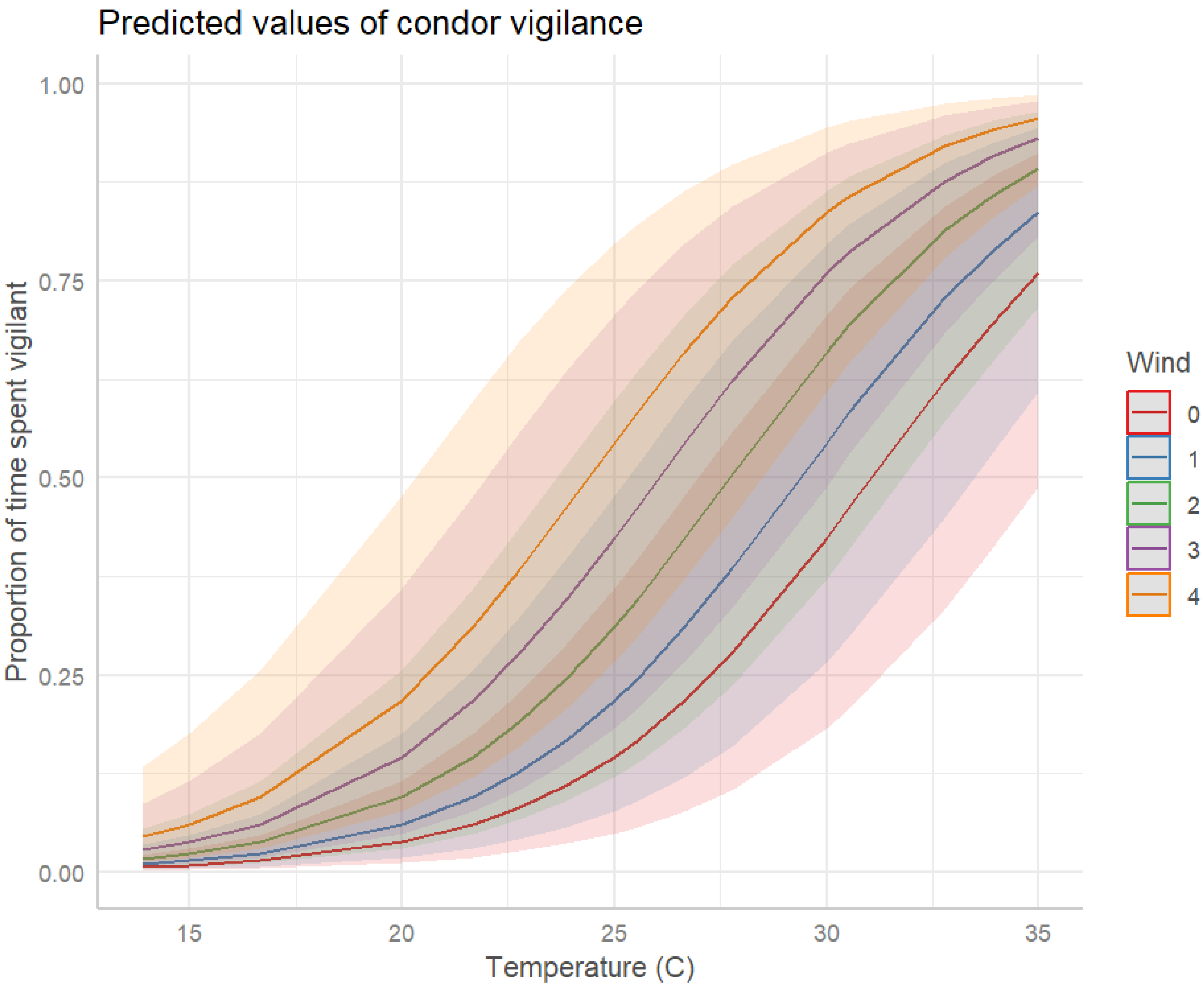

Figure 3.2. Condor proportion of time spent vigilant across temperatures and wind speed on the Beauford scale, in Iron Co., UT, May - September 2022 - 2023.

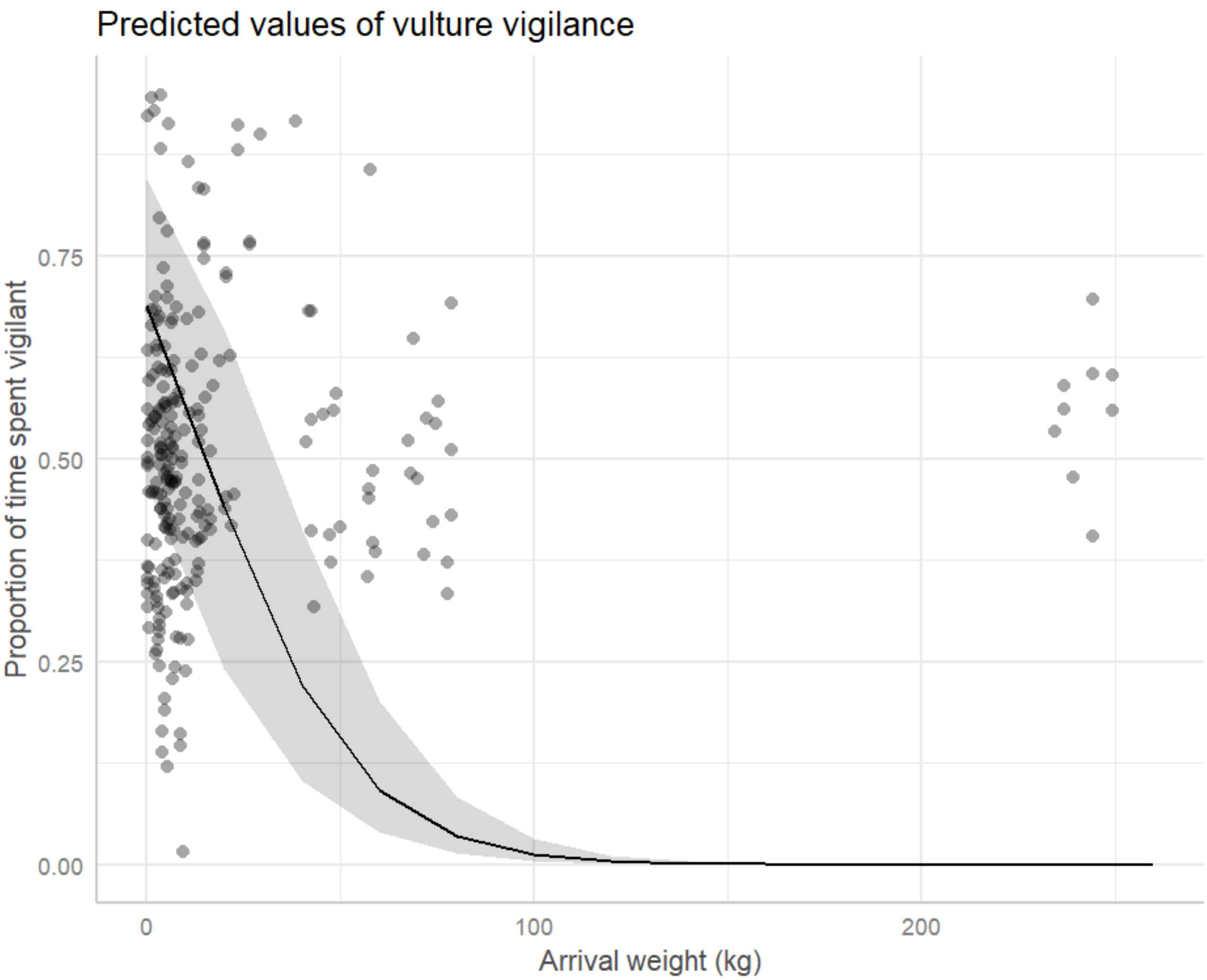

Figure 3.3. Turkey vulture proportion of time spent vigilant modeled from the kg of carrion remaining at the beginning of each visit, Iron Co., UT, May - September 2022 - 2023.

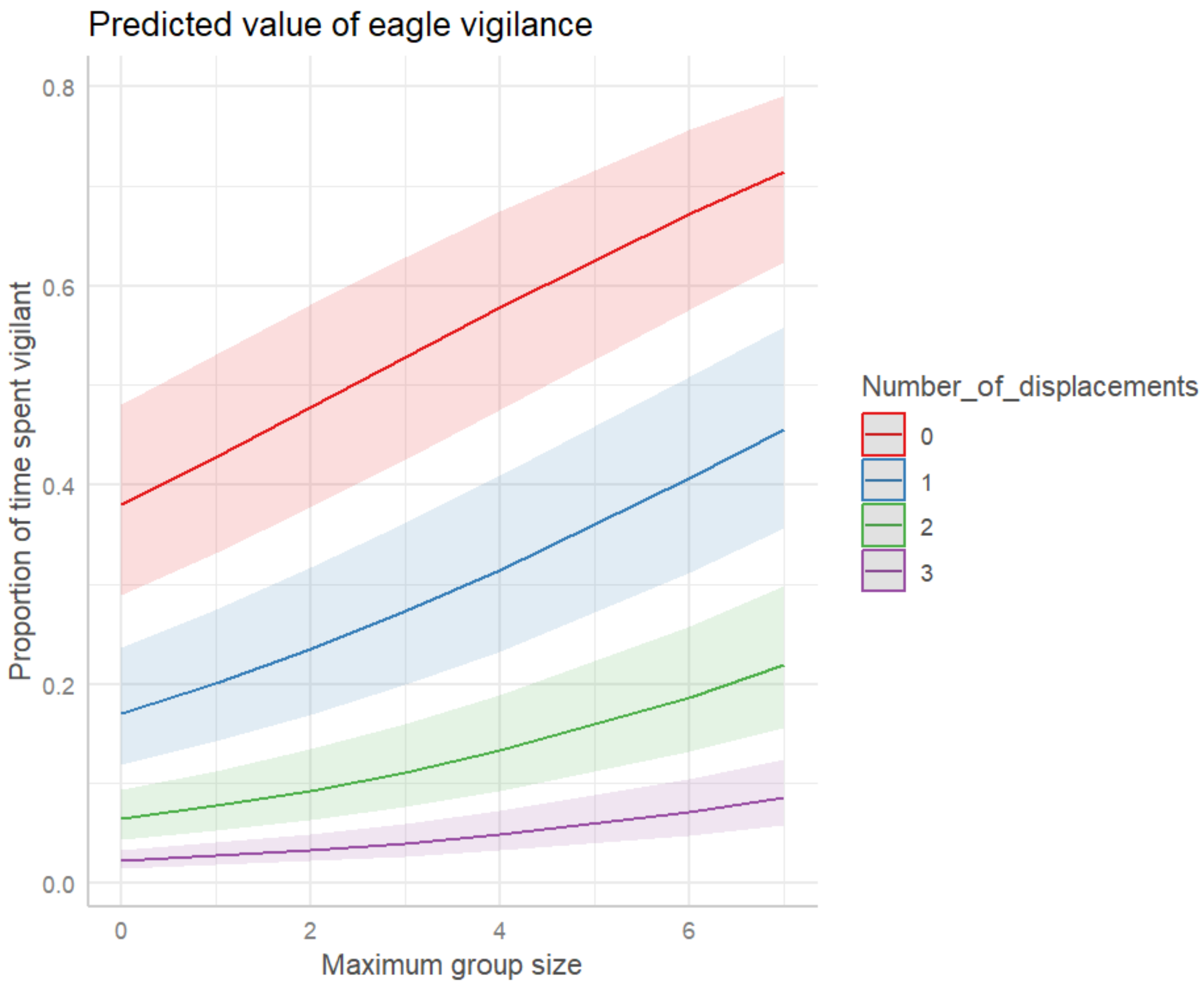

Figure 3.4. Golden eagle proportion of time spent vigilant against maximum group size at focal individual arrival or departure from the carcass and number of displacements caused by focal individual, in Iron Co., UT, May - September 2022 - 2023.

CHAPTER IV

COMPETITIVE INTERACTIONS BETWEEN CALIFORNIA CONDORS AND AVIAN SCAVENGERS IN SOUTHERN UTAH

Abstract

California condors (*Gymnogyps californianus*) were reintroduced to southern Utah and northern Arizona in 1996, and their presence at carcasses may adversely impact the historic scavenger community. Unlike other avian scavengers in Utah, condors are large, feed in groups, and may command food resources by excluding other scavengers. Little is known about foraging patterns of condors and their competitors, including interactions among scavengers. I deployed trail cameras on 76 carcasses and recorded scavenger behavior, including arrival rates, carrion consumption, displacements, and visit duration. Condors arrive at carcasses within an hour of the first scavenger and on average consume over half the carrion, leaving little for other scavengers. When condors arrived, 27% of the carcass had been eaten, compared to 78% when condors departed, while consuming approximately 15 kg of carrion. Golden eagles (*Aquila chrysaetos*) and condors displaced each other when simultaneously present at a foraging site and visitation rates of turkey vultures (*Cathartes aura*) declined after condors had visited a carcass. As condor populations continue to increase, densities of eagles and vultures may decline as a result of additional competition from condors for carrion.

Introduction

As part of California condor (*Gymnogyps californianus*) recovery, 4 distinct populations have been reintroduced in western North America. Each of these recovery areas have returned condors to parts of their historic distribution with the help of yearly releases. The 2 populations in California have increased across time, and the condors became less dependent on carrion offered at release sites and are more likely to be absent from the monitoring area (Bakker et al. 2017). The same pattern of increasing independence across time holds true for the population of condors in Arizona and Utah (T. Hauck personal communication). Condors are increasingly scavenging on wild carcasses and competing with other scavengers in their foraging area. In Utah, potential avian competitors of the California condor include golden eagles (*Aquila chrysaetos*, hereafter eagle), turkey vultures (*Cathartes aura*), and common ravens (*Corvus corax*). Mammalian scavengers include striped skunks (*Mephitis mephitis*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), black bears (*Ursus americanus*), and mountain lions (*Puma concolor*).

Despite competitive pressures, coexistence among species occurs through niche partitioning and differential survival. Turkey vultures can withstand higher lead levels in their blood than other avian scavengers (Carpenter et al. 2003), and so may feed on carcasses shot by hunters with fewer consequences than other species, including condors (Bakker et al. 2024). Andean condors (*Vultur gryphus*) have a large niche overlap with competitors when competing in landscapes with several other species, and their coexistence with vultures may be due to behavioral, temporal, or spatial partitioning (Silverthorne et al. 2020). Behavioral partitioning can include differences in arrival times, feeding strategy, or consumed parts of carcasses (Travaini et al. 1998, Byrne et al. 2019).

In turkey vultures, arrival order and timing of arrival may play an important strategic role in competing for carrion. Turkey vultures have a well-defined sense of smell and often find carcasses first (Wallace and Temple 1987). Their ability to locate carcasses quickly by themselves allows them to feed before the arrival of dominant scavengers, such as black vultures (*Coragyps atratus*). Earlier arrival may also mean turkey vultures can feed more efficiently, as later scavengers may only be feeding on more difficult ligaments and meat closer to bones. Black vultures have a poor sense of smell, relying instead on visual detection of carcasses. Black vultures are known to be more aggressive and feed in groups, often arriving after and displacing turkey vultures (Wallace and Temple 1987, Byrne et al. 2019). Like black vultures, condors do not have a well-defined sense of smell and may be dependent on other scavengers to locate carrion, following them to carcasses. Condors feed in groups, and the presence of one condor often attracts others, compounding the impact of condors on other scavengers. Therefore, the time before condor arrival at carcasses determines the amount of time that other scavengers have to feed uninterrupted (Travaini et al. 1998).

Little is known about condors' patterns of competition and success in competing for carrion. Andean condors are able to compete with mountain lion for their kills (Elbroch and Wittmer 2013), and condors may impact avian and mammalian scavenger communities if condors are dominant scavengers. As large, social birds, condors may have a greater ability than turkey vultures to intimidate other scavengers at carcasses. The presence of condors may thus have a disproportionate impact on other scavengers. Condors are generally dominant over vultures and common ravens, but interactions with eagles are less predictable (San Diego Zoo Wildlife Alliance Library 2024). Golden eagle populations have experienced fluctuations across their range and have been declining in Utah, in part due to food shortages. Supplemental feeding programs for eagles have been proposed and implemented in Utah (HawkWatch International 2023), but may be hindered within the condor's range if condors outcompete eagles at carcasses. However, intraspecific competition tends to be stronger than interspecific competition and may have greater impacts on an individual's ability to forage (Houston 1988).

The amount of carrion eaten by an individual is crucial for understanding competition among scavengers. A condor is able to consume ~1.5 kg of carrion at a time, usually filling its crop in 20 minutes and only feeding every few days (San Diego Zoo Wildlife Alliance Library 2024, U.S. Fish and Wildlife Service 2024). Estimates on carrion consumption were determined from captive populations of condors, but wild populations of birds may exhibit similar nutritional requirements (Komen 1992). Golden eagles only need 0.7 kg of food a day, which is mostly provided by carrion (Brown and Watson 1964). As smaller scavengers, turkey vultures in captivity only require 0.1 kg of food (Tabaka et al. 1996). Although few studies quantify the availability of carrion, it is likely that in high-elevation areas in Utah, there is a pulse of ungulate carcasses during the winter due to thermal stress and lack of browse (Moleón et al. 2019). These pulses can be stabilized across time by dominant predators, such as mountain lions and wolves, as they create carcasses regularly (Moleón et al. 2019). Competition will likely be more intense at times or in areas where carrion is scarce and scavenger populations are denser, such as during raptor migration in spring and fall. Turkey vultures are willing to forage farther from roosting sites and at smaller carcasses than black vultures, which can disperse the impact that turkey vultures have across a larger area and allow turkey vultures to access carcasses with fewer competitors (Coleman and Fraser 1987). Although dominance at a carcass may be based on body size of species, acquisition of carrion can change depending on abundance or aggressive behavior of a species at a carcass (Halley and Gjershaug 1998, Carrete et al. 2010). If species are able to obtain food regardless of dominance hierarchies established through aggression, it may allow for coexistence. However, the necessity of several individuals present at a carcass to gain control and feed may create issues if populations drop below some threshold.

The frequency of visits and duration of each visit measure the use of a carcass in different ways, as scavengers may make several small visits rather than one long visit, but still consume an equal amount of carrion across visits. The cumulative amount of time at a carcass can reflect efficiency and the amount of carrion eaten. Additionally, visit rates of scavengers can be affected by the prior presence of dominant scavengers. For example, even when not simultaneously present, previous wolf (*Canis lupus*) use of carcasses can influence use and behavior of other scavengers (Klauder et al. 2021). Dominant scavengers are hypothesized to repel subordinate scavengers, but the interactions between scavengers may be more complicated, as scavenger visits may increase with other species' visits or have no impact. For example, individual golden eagles are more likely to make additional visits if more eagles use a foraging site (Watson et al. 2019). Researching the interactions between condors and their competitors is crucial to understanding the potential for condors to impact the scavenger community; and if so, which species are most affected. In this study, I quantify the impacts of condors on other scavengers using a variety of measures, including arrival time compared to other scavengers, quantities of carrion eaten, displacement of competitors during visits, and visit duration and rates across scavengers.

Methods

Study site

Cedar Mountain is a plateau in southwestern Utah at 2600 m elevation used as summer pastures for sheep (Fig. 4.1). California condors arrive on Cedar Mountain in mid-June and remain until October, coinciding with sheep grazing activity on the mountain (Palmer 2009). On Cedar Mountain, condors primarily feed on sheep carcasses due to the high availability of this food source during this time period (T. Hauck personal communication). In summer 2023, the Arizona-Utah population of condors included 95 individuals, all from a single release site in Vermilion Cliffs, Arizona. Other scavengers on Cedar Mountain potentially competing with condors include mountain lions, black bears, red foxes, coyotes, striped skunks (*Mephitis mephitis*), turkey vultures, golden eagles, and common ravens.

Study design

From May to September of 2022 and 2023, I systematically searched for sheep mortalities on pastures on Cedar Mountain by walking along sheep trails from bedding areas to resting areas (similar to Palmer et al. 2009) and investigated any reports of mortalities from ranchers and shepherds. At the beginning of each field season, I consulted with sheep producers and confirmed the location of bedding grounds on each pasture, as most sheep are killed while resting. I found fewer carcasses than expected during the summer of 2022, so I searched for mule deer (*Odocoileus hemionus*) carcasses while driving over Utah State Route 14 on the ~60 km between Cedar City and Duck Creek Village, Utah. In addition, I obtained locations of roadkill from Utah Division of Wildlife Resources. In 2022, to supplement the sample size of naturally occurring carcasses, I distributed ewe and lamb carcasses obtained from ranchers within the study area. In 2023, I obtained and froze lamb carcasses from sheep producers during spring lambing (April-May) in anticipation of summer fieldwork, and primarily relied on setting out lamb carcasses rather than expanding efforts to search for mortalities in pastures.

To determine where to place supplemental carcasses, I used ArcGIS (ESRI 2023) to view pastures that I had landowner permission to access. I used stratified random sampling within accessible areas, defined as slope <45°, within 5 km of a road, and >100 m from any buildings, to randomly generate an equal number of points across vegetation types. I used LANDFIRE rasters (with 30 m resolution; LANDFIRE 2020) to collect data of existing vegetation type. I combined existing vegetation types broadly into 10 major categories following Rivers et al. (2014) to create classifications relevant to condors that encompassed vegetation types likely to be encountered. These categories included deciduous forest, evergreen forest, savanna, grassland, sparse vegetation, shrubland, modified land, wetland/riparian, agriculture, and unsuitable habitat (e.g., open water). This classification method is similar to those used in Stoms et al. (1993) for condor sightings. Random location also had to be >200 m from each other. These random locations were used when placing carcasses within a pasture.

In 2022, when I found roadkill on the state highway, I collected it and relocated it as soon as possible to the next potential location on Cedar Mountain. Every week over the summer of 2023, in addition to locating naturally occurring sheep carcasses, I set out ≥2 carcasses, each consisting of ≥1 frozen lambs (total initial weight 3.2 - 20.4 kg). Carcasses that I set out were placed ≥2 km from the nearest active carcass to avoid overlap in detection by scavengers based on proximity (similar to Speziale et al., 2008).

I used trail cameras (Campark T20 Mini Trail Camera, Campark Electronics, Portland, OR) placed on trees, fence posts, or staked metal poles, approximately 1 m off the ground (the average scavenger height) to record visits from scavengers. I scheduled cameras to take 30-s videos with 5-s rest intervals whenever motion was detected, with low sensitivity to minimize videos of vegetation moving with wind. I used 16-GB to 64-GB SD cards (SanDisk, Milpitas, CA). I placed 2 cameras facing the carcass, one ~3 m away and one ~5 m away, at 90° from each other, to minimize missed scavenger visits from size differences, scavengers dragging carcasses in different directions, and camera failure. I tied carcasses with a cable formed into a snare and staked them into the ground with 45-cm-long steel stakes to prevent the carcass from being dragged out of the cameras' frame. I weighed carcasses when setting them out using a scale if <25 kg and used weights found in published literature if >25 kg.

I checked camera batteries and SD cards at least weekly and replaced these as needed. Trail cameras were continuously active at carcasses until carcasses were at least 75% consumed, had been out for at least 7 days, or reached such an advanced stage of decay that most mammalian and avian scavengers would not feed on the carcass due to putrefaction. I calculated the proportion of the carcass consumed by visual estimation during these checks, serving as known reference points compared to video estimation of carcass consumption.

At the start of every scavenger visit, I recorded time, weather, species and number of other individuals (combined across all species present), and proportion of the carcass that had already been eaten. Time was displayed on the video from the camera. Weather included wind, visually estimated from videos using the Beaufort scale; temperature, from the camera; and cloud cover, visually estimated as a percentage. Visit number ascended with each visit from any scavenger per carcass. When the scavenger left, I recorded the time, species and number of other individuals, and proportion of the carcass consumed. The maximum of number of other individuals across arrival and leaving from each visit was used as maximum group size. Arrival weight was calculated from the percent eaten at the time a scavenger arrived and initial weight when the carcass was established. For each condor group's visit to a carcass, I also recorded the size of any openings in the carcass each time a scavenger arrived and then again at its departure. Size was visually estimated from videos into 4 categories: intact, small openings (allowing one bird to feed at a time, <20 cm), large openings (allowing >1 bird to feed), and hideless.

Visits were defined as any scavenger in the frame for any length of time, regardless of feeding activities. If a scavenger left the frame and was not seen for >15 minutes afterwards, the visit was ended when the scavenger exited from view, and any subsequent reentry in frame was counted as a new visit. When individuals had unique tags (i.e., condor wing tags or dog collars), their identity was also recorded. Individuals that were not identifiable, such as vultures, were kept track of through their location and movements.

I created an ethogram within Behavioral Observation Research Interactive Software (BORIS, Friard & Gamba, 2016) to record behavior from the collected videos. For each visit by any scavenger, I manually recorded feeding, vigilance, and other behaviors (including moving, preening, and aggression), which were summed individually. All these behaviors were combined together as time of known behavior.

Feeding was defined as head down with the beak touching the carcass. Vigilance was defined as head raised without the bird moving. Additionally, time of behavior that could not be determined, if the individual was out of frame for a short time or too far away to confidently categorize, was recorded as unknown and was added to the time of known behavior to create time of all behaviors. Displacements were defined as one individual leaving due to aggressive actions of another, such as pecking, lunging, and chasing. Total displacements caused by an individual were summed for each visit. Displacements of the same individual multiple times during one visit were counted as separate instances.

Means with standard deviations were applied when appropriate. I performed a Kruskal-Wallis test on feeding time across scavenger species (Kruskal and Wallis 1952). I ran a linear regression on the amount of the carcass eaten during each condor group's visit against condor group size and duration. The model did not display good fit using DHARMa (Hartig 2022), so I created models with each variable individually, which both displayed adequate fit. I used AIC to compare the two models and only report the results of the top model (Akaike 1987), condor group size against amount of carrion eaten. I used an analysis of variance (ANOVA) and Tukey HSD to determine differences across rates of displacement and arrival between species.

Results

I recorded scavenger behavior at 76 carcasses. Condors appeared at 12 carcasses, and mean number of condors at any one carcass was 13.5 individuals (SD = 14.2). From 47 individual visits, the average duration spent at a carcass was 17.6 minutes (SD = 18.9). However, condors tended to arrive and leave in groups, so groups of condors were used as the sampling unit rather than individual visits. No solitary feeding events by condors were observed. When condor activity was analyzed as a group, 13 group visits lasted on average 1.11 hr (SD = 0.05). Vultures and eagles did not tend to arrive and leave as a cohesive group, so I used visits from each individual as my sampling unit, because I could consider visits independent from each other.

Time between carcass establishment and first visit by each species was slightly significant across species (P = 0.06). Interestingly, mean time to first visit was higher for vultures than for eagles and condors; these differences were not significant when tested pairwise (Table 4.1). Vulture visitation rate was significantly lower after a group of condors visited (0.03 visits/hour) compared to before condor arrival (0.32 visits/hour, P = 0.03), while eagles were not affected significantly (before: 0.24 visits/hour, after: 0.03 visits/hour, P = 0.08).

In 13 instances of groups of condors arriving, 9 carcasses already had small openings, 3 had large openings, and one was hideless (as condors had visited previously). When condors left, 1 carcass had small openings, 4 had large openings, and 8 were hideless. For the only case in which condors left the carcass with small openings, there was only one condor present and that bird spent less than a minute and left without feeding on the carcass. All scavenger species observed on the cameras could feed on carcasses before condors opened the carcass. Condor activity was not required to enable vulture and eagle scavenging at a carcass, because both species were capable of creating and enlarging openings in carcasses to feed without difficulty. Vultures and eagles had repeated visits (across different individuals and days), wherein they progressively opened a carcass.

In 13 instances of video footage of condor groups at 12 carcasses, on average 27% (SD = 27%) of the carcass previously had been eaten when condors initially arrived, and 78% (SD = 28%) of the carcass was eaten when condors left. Before condors appeared, an estimated average of 33.8 kg (SD = 36.2 kg) of carrion remained, and only 15.7 kg (SD = 30.2 kg) remained when condors departed. The amount of carrion eaten during each group's visit was positively correlated with condor group size during the visit (P = 0.02, Table 4.2). The proportion of carcasses eaten during a visit was ~6% for both vultures and eagles. On average, eagles consumed 1.4 kg (SD = 1.4 kg) of carrion during a visit and vultures consumed 1.0 kg (SD = 1.5 kg) during a visit.

Eagles made an average of 7 visits to a carcass, vultures made 10 visits, and condors made 7 visits. Multiplying average visit numbers with average amounts of carrion consumed during a visit to obtain total carrion consumption by a species, eagles consumed 9.7 kg and vultures 9.4 kg. I excluded condors from this as condors fed in groups, and visits were often different individuals overlapping rather than temporally separate visits. Sample sizes are smaller for coyotes and foxes, but they consumed 7.9 kg and 2.3 kg, respectively. Ravens were only present at 3 carcasses, but their average consumption was 8.7 kg, across 27, typically short, visits per carcass.

Overall feeding times for condor-raven, condor-vulture, and eagle-raven comparisons are significantly different (Appendix C: Table C1), with the larger species eating for longer in each case (Table 4.3). However, proportion of time spent feeding was not significantly different across species. The difference in total feeding time therefore comes from a difference in visit duration; while condors do not have higher proportion of time spent feeding while at carcasses, they spend longer during each visit than eagles, ravens, and vultures (Table 4.4).

I evaluated competition between species at carcass sites; in most cases of competition, individuals displaced conspecifics more than other species (Table 4.5). In terms of comparing frequencies of displacement across species, the only statistically different rate of displacement was between vultures and condors ($P = 0.008$), with vultures exhibiting a greater displacement rate of any other scavenger than condors (Table 4.6). Anecdotally, condors will quickly displace other avian scavengers, which usually leave the foraging site, prohibiting any future displacements. Vultures will occasionally stay near the carcass, remaining vigilant and waiting for condors to leave. Condor behavior is likely more impacted by presence of conspecifics (and number of conspecifics) than by other species. Foxes and coyotes primarily visited at night, and I did not record any interactions between condors and mammals.

Discussion

Condors are known to feed socially (Sheppard et al. 2013), and I never observed condors feeding individually. Previous estimates on group sizes were around 12 individuals foraging together (Sheppard et al. 2013). My maximum group size was 42 individuals, almost half of the Arizona-Utah population of condors. The condors' gregarious feeding patterns emphasize the potential harm of even one carcass contaminated with lead, and challenges associated with keeping condors from feeding on dangerous carrion.

The average time a condor spent at a carcass was 17.5 minutes, is much shorter than previous estimates of >2.5 hours (Sheppard et al. 2013), and duration of time spent by groups is even shorter. This is probably influenced by the smaller size of carcasses in this study. However, it may also be caused by increased depredation risk at naturally found carcasses – previous studies have analyzed condor behavior at feeding stations, which are visited by condors often and are familiar to condors. Sheppard et al. (2013) report average percent of time spent feeding by condors while at a carcass as 69%, while the percent of time spent feeding was 46% for this study. The decreased time spent feeding at carcasses supports the suggestion that condors are displaying greater feeding efficiency at potentially risky sites. Condors can spend most of their time in safe areas, preening and socializing, with limited time at risky carcasses (U.S. Fish and Wildlife Service 2024).

Condors could act as facilitators for other scavengers, if the condors open carcasses that other scavengers could not open. However, during this study, other scavengers were able to obtain meat on their own. This is possibly because I primarily used sheep and deer carcasses, whose hides are not especially thick. Cattle have thicker skin and may pose more of a challenge to avian scavengers. In addition, condors ate the majority of a carcass, especially when the carcass was small. This leaves less carrion for other scavengers that arrive after condors, even if the carrion was now more easily accessible as a result.

Indeed, vultures were less likely to arrive after condors had visited a carcass, compared to before condors arrived. This may be because vultures avoid condors or because there is little meat available after condors feed. Regardless, the lower rates of visits by other scavengers after condors have been to a carcass demonstrates the adverse impact of condors on other species. Condors are able to monopolize carcasses, so vultures may change their space-use to exploit other carcasses to minimize foraging losses associated with competition from condors.

Vultures made almost 10 visits on average to a carcass, while eagles and condors made 7 visits. The visits made by vultures and eagles may have been by the same individual, but I had no way of telling individuals of the same species apart from each other. Most condor visits were by different individuals at any given carcass, and individuals only made multiple visits at a single carcass, coming and going within a larger group visit. The carrion removed during a vulture visit was much less than when condors were present, and repeatedly visiting foraging sites may reflect vulture's lower costs of landing and takeoff compared to those of larger condors, as well as the smaller crops of vultures. This agrees with my finding that vultures spend significantly less time feeding than condors. The strategy of shorter visits employed by turkey vultures is dependent on carrion persistence, and vultures could be disproportionately affected when condors arrive and consume the majority of a carcass.

Smaller species on average fed for less time during a visit than larger species, which reflects known dominance hierarchies in other assemblages of avian scavengers (Moreno-Opo et al. 2020). However, previous studies have also reported several species of obligate scavengers feeding for more time than facultative scavengers (Moreno-Opo et al. 2016). Here, I found no such pattern between obligate and facultative scavengers. When carrion is available, it may be a preferred food source, so that facultative avian scavengers feed for similar amounts of time as obligate scavengers.

The mean amount of time between carcass establishment and the first arrival of a species was not significantly different among any species. However, condors were never the first species to a carcass. Vultures had a surprisingly long average time to arrival, because they often visited carcasses that other scavengers did not appear at, which skewed the average first arrival time. These carcasses may have been harder to detect due to size or habitat.

Differences in competition ability can cause the weaker competitor's population size to decline or remain low, and vultures have a demonstrated ability to regulate mammalian and avian populations (O'Bryan 2019). Condors have an impact on other avian scavengers, namely vultures and eagles. This stems from direct competition at carcasses, where condors enter into disputes with eagles that could be energetically expensive and dangerous. Vultures decrease their visitation rate to carcasses after a group of condors have been present, limiting the usefulness of carcasses after condors visit. Vultures therefore have a limited amount of time to feed before condors arrive. On average, condors arrived 34 hours after carcass establishment. The median time between arrival of the first avian scavenger and condors was less than an hour. In addition, scavengers face indirect impacts from condors monopolizing carrion; on average, condors consumed over half the carrion at a foraging site, leaving little for other scavengers. These direct and indirect impacts may cascade through the scavenger community, as some species are better equipped to overcome the challenges posed by condors. These adverse impacts should increase in the future as condor populations expand. Unequal competition not only keeps mammalian scavenger populations low, but also can determine the population size of species within avian scavenger communities.

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Tables and Figures

Table 4.1. Pairwise comparisons of avian scavenger time to arrival at carcasses on Cedar Mountain, Iron county, Utah, from May – September 2022, 2023, using a Tukey Honest Significant Difference test. Diff describes the difference in means, with lwr describing the lower confidence bound and upr describing the upper confidence bound. All bounds include 0, and no paired species show statistically significant differences.

	Diff	Lwr	Upr	P value
Eagle - condor	-0.08	-2.15	1.99	1.00
Vulture - condor	1.36	-0.52	3.25	0.20
Vulture - eagle	1.44	-0.22	3.10	0.10

Table 4.2. Results from linear regression describing effects of condor group size on kg of carrion eaten during the condor group's visit, Iron County, Utah, May – September 2022, 2023. Multiple R-squared value was 0.3822.

	Estimate	Standard error	T value	Pr(>|t|)
(Intercept)	5.85	6.75	0.87	0.40
Condor numbers	0.95	0.37	2.61	0.02

Table 4.3. Sample size, mean and standard deviations of feeding times (in seconds) by species during a single visit to carcasses in Iron County, Utah, May – September 2022, 2023. Condor-raven, condor-vulture, and eagle-raven differences are statistically different from each other.

Species	N	Mean	Standard deviation
Condor	46	499	672
Coyote	3	53	42
Domestic dog	4	36	32
Eagle	77	328	318
Fox	3	116	106
Great horned owl	1	37	NA
Raven	74	121	99
Skunk	1	50	NA
Vulture	218	234	263

Table 4.4. Sample size, mean and standard deviations of total visit duration, in seconds, by species at carcasses in Iron County, Utah, May – September 2022, 2023.

Species	N	Mean	Standard deviation
condor	69	1079	672
vulture	220	552	263
eagle	73	529	318
raven	75	336	99
fox	3	285	106
domestic dog	5	181	32
coyote	4	117	41.99

Table 4.5. Numbers of displacements recorded during videos of scavengers feeding on carcasses, Cedar Mountain, Iron County, Utah, May – September 2022 and 2023. Columns indicate the species initially on the carcass, rows indicate the species that arrived and displaced the original animal on the carcass.

	Vulture	Eagle	Condor
Vulture	77	0	0
Eagle	1	2	8
Condor	0	1	21

Table 4.6. The results of a Tukey's test of honest significant differences comparing displacement rates between two species scavenging on carcasses on Cedar Mountain, Iron County, Utah, May – September 2022, 2023. Each species has a displacement rate (displacements/hour) and these rates are being evaluated for statistically significant difference across all species pairs, not displacements of one species by the other. P <0.05 indicates statistical difference, adjusted for multiple comparisons. Diff is the difference in rates, lwr is the lower confidence bound, and upr is the upper confidence bound.

	Diff	Lwr	Upr	P value
Eagle - condor	0.65	-0.39	1.70	0.36
Raven - condor	-0.10	-1.64	1.43	1.00
Vulture - condor	0.82	0.16	1.49	0.01
Raven - eagle	-0.76	-2.43	0.91	0.64
Vulture - eagle	0.17	-0.76	1.10	0.96
Vulture - raven	0.93	-0.53	2.39	0.35

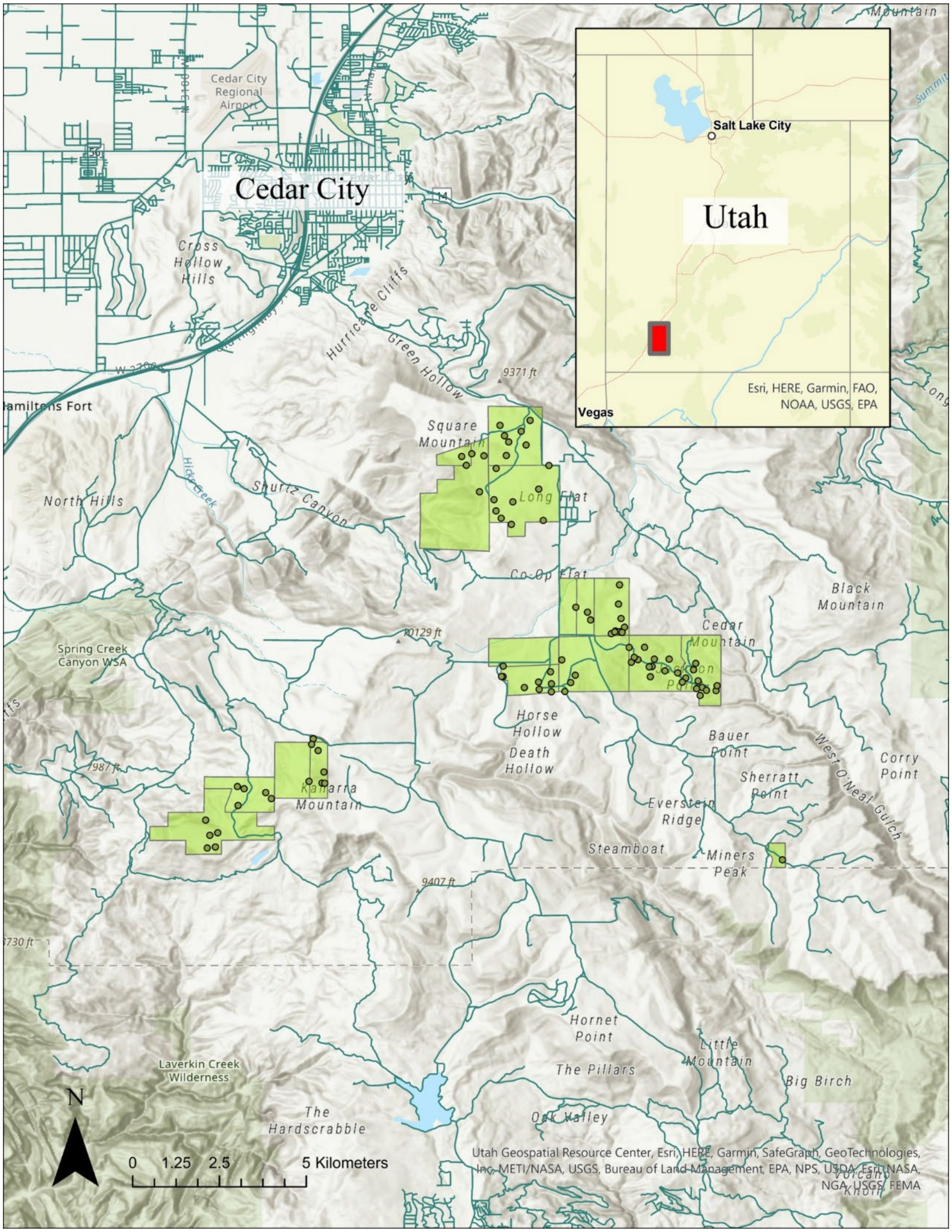

Figure 4.1. Location of study site in southern Utah, USA, May - September 2022, 2023. Carcass locations are indicated within private pastures, which are denoted in green.

CHAPTER V

CONCLUSIONS

In this thesis, I investigate the foraging niche of scavengers on Cedar Mountain, the behavioral flexibility of avian scavengers across habitats, and the impacts of reintroduced condors on other species. Every California condor (*Gymnogyps californianus*) from 1987 to 1992 existed in captivity, and captive breeding programs with subsequent reintroductions are an important tool when the continued survival of a wild population is unlikely. At the same time, reintroductions of dominant species can cause ecological cascades. This serves as the first study investigating the potential of condors to have similar effects on scavenger communities.

Chapter 2 discusses the foraging sites of condors. The last probable sighting of a condor in Utah or Arizona was in 1924, and they were reintroduced at Vermilion Cliffs, Arizona, in 1996 (Arizona Game and Fish 2024). Since then, the population and their range have increased. Exploratory forays soon after initial reintroductions have gone as far as Flaming Gorge, Wyoming, but condors have settled into their primary foraging areas, including Cedar Mountain. From feeding sign and videos at carcasses (primarily sheep, *Ovis aries*, and deer, *Odocoileus hemionus*), I determined that condors select for lower understory cover, but show no preference or avoidance of roads. Most sheep mortalities occurs on resting areas, which often are grazed down and have little understory cover, offering a safe and accessible source of carrion. I was not able to include additional covariates to the model without potentially overfitting the data, as condor attendance at carcasses was rare. Future studies could compare the effects of understory height, canopy coverage, and carcass weight on condor presence.

I ran similar analyses on other common species of scavengers to estimate overlap in foraging site preferences. Golden eagles (*Aquila chrysaetos*, hereafter eagle) selected for higher understory cover far from roads, and for lower understory cover when close to roads, which could lead to human-mediated conflict between eagles and condors. Turkey vultures (*Cathartes aura*, hereafter vulture) did not select for any vegetation or carcass variables, but were more likely to visit carcasses earlier in the season. Ravens (*Corvus corax*), coyotes (*Canis latrans*), and foxes (*Vulpes vulpes*) did not display any strong selection of carcasses. These species may use carcasses in areas of greater understory cover as needed if competition from condors is strong, and future research should compare their space use in areas dominated by or without condors.

Alternatively to complete avoidance of carcasses deemed unsafe, scavengers may employ behavioral tactics, such as increased vigilance or shifted temporal use of carcasses, to match energy requirements with perceived risk. Chapter 3 delves into behavioral flexibility of avian scavengers at carcasses, using a lens of risk avoidance or tolerance. Condors, as dominant scavengers, may select the safest carcasses to feed on. Competition from condors may drive avian scavengers to habitats that are less safe, especially as carcasses attract potentially dangerous mammalian scavengers and predators. Avian scavengers may react to suboptimal feeding sites by increasing vigilance, at the expense of feeding. All avian scavengers modified their behavior based on different environmental variables, which suggests different yet successful strategies for balancing energetic demands and safety across the avian scavenger guild. Condors did not spend a greater proportion of time vigilant than other species did, but increased vigilance with increasing wind speed and temperature, which may be related to difficulties in taking off if predators were to approach. Eagles increased vigilance with increasing group size and displacements caused, indicating the impact of other individuals present during a visit. Vultures decreased vigilance at larger carcasses, potentially because of the trade-off between feeding and vigilance, and the need to feed as much as possible before other scavengers arrive. Future directions include incorporating a range of scavenger communities when characterizing a species' behavioral flexibility, as well as investigating vigilance at predator kills, which may be perceived as more risky. Additionally, individuals within a species may react differently to levels of perceived risk; sex, age, and breeding status could all impact responses. I was not able to collect information on individual demographics on eagles and vultures, but future studies could tag and age birds in addition to assessing behavior.

Chapter 4 summarizes the impact of condors on other scavengers. Condors consume ~50% of the carcasses they visit and feed on, and each individual only feeds for 8 minutes on average. This results in rapid depletion of the available carrion, leaving little for other scavengers once condors have visited a carcass. Condors were never the first scavengers to arrive, but arrived less than an hour after the first scavenger. Scavengers therefore have little chance to consume carrion at carcasses that condors utilize. Vulture visit rates decline after condors visit foraging sites, further highlighting the impact of condors. When simultaneously present at foraging sites, condors and eagles displace each other, although most interactions are among conspecifics. The population densities of eagles and vultures may decline as a result of additional competition for carrion, so the competitive pressures of condors on other scavengers should be monitored. In addition, competition from condors or other scavengers may drive predators away from their kills, leading to higher kill rates, and monitoring the predator population and cache sites.

References

Arizona Game and Fish. 2024. California condor recovery. https://www.azgfd.com/wildlife-conservation/conservation-and-endangered-species-programs/california-condor-recovery/. Accessed on 05 March 2024.

APPENDICES

APPENDIX A

CHAPTER II SUPPORTING INFORMATION

Table A1. Mean, standard deviation, and t-test results across all habitat variables measured, comparing foraging sites that condors attended to those without condors. Ordinal day established is the number of days since Jan 1st of that year that I established the carcass. Average canopy is the average of canopy closure measured across all cardinal directions. Distance to predator cover is the nearest distance at which a board (0.9 m by 0.3 m) could be completely obscured. Profile A through E denotes half-m sections of understory vegetation density, with E being the lowest section. Average profile is the mean of all sections for a given carcass. Average vegetation height was the average of 15 measurements of tallest vegetation, taken each meter in a random direction from the carcass. Distance to paved and all roads were digitally calculated using ArcGIS using road layers and GPS points of the carcass. Initial weight is the starting weight of the carcass when established, either weighed on site (<25 kg) or estimated from published accounts (> 25 kg). Max ascent was the highest value recorded for ascent, and min ascent is the lowest. Ascent was measured in all cardinal directions, as the lowest angle from horizontal that vegetation could be cleared. Northness and eastness were derived from aspect, measured at the carcass site.

Variable	Mean condor absent	Mean condor present	SD condor absent	SD condor present	t-value	df	P-value
Ordinal day established	206.87	208.95	36.91	34.68	-0.23	34.01	0.820
Average canopy	17.17	0.43	26.88	1.90	4.87	62.86	0.000
Distance to pred cover	15.58	25.75	15.99	13.70	-2.77	37.12	0.009
Profile A	0.81	0.05	1.65	0.22	3.52	67.46	0.001
Profile B	0.84	0.05	1.63	0.22	3.70	67.57	0.000
Profile C	0.81	0.05	1.51	0.22	3.81	68.53	0.000
Profile D	1.23	0.20	1.67	0.52	4.23	79.99	0.000
Profile E	3.05	2.00	1.69	1.69	2.42	32.31	0.022
Average profile	1.35	0.47	1.40	0.42	4.35	79.77	0.000
Slope	6.53	7.45	4.92	6.82	-0.56	25.69	0.583
Elevation	2782.68	2794.20	97.10	77.39	-0.54	39.99	0.591
Average veg height	169.28	15.05	323.87	12.66	3.74	61.57	0.000
Distance paved road	932.27	853.51	539.10	400.19	0.70	43.15	0.488
Distance all road	380.05	263.49	295.34	229.54	1.83	41.07	0.074
Initial weight kg	23.30	41.91	36.94	51.44	-1.50	25.63	0.146

Table A1 (cont.)

Variable	Mean condor absent	Mean condor present	SD condor absent	SD condor present	t-value	df	P-value
Max ascent	32.02	14.75	28.38	13.03	3.73	70.33	0.000
Min ascent	7.48	0.85	12.84	2.18	3.90	70.61	0.000
Northness	0.19	-0.06	0.62	0.68	1.45	30.13	0.159
Eastness	0.24	0.12	0.73	0.76	0.63	31.11	0.535

Table A2. Pearson's correlation matrix across all habitat variables measured. Ordinal day established is the number of days since Jan 1st of that year that I established the carcass. Average canopy is the average of canopy closure measured across all cardinal directions. Distance to predator cover is the nearest distance at which a board (measuring .9 m by .3 m) could be completely obscured. Profile A through E denotes half-m sections of understory vegetation density, with E being the lowest section. Average profile is the mean of all sections for a given carcass. Average vegetation height was the average of 15 measurements of tallest vegetation, taken each meter in a random direction from the carcass. Distance to paved and all roads were digitally calculated using ArcGIS using road layers and GPS points of the carcass. Initial weight is the starting weight of the carcass when established, either weighed on site (if <23 kg) or estimated from published accounts (if more than 23 kg). Max ascent was the highest value recorded for ascent, and min ascent is the lowest. Ascent was measured in all cardinal directions, as the lowest angle from horizontal that vegetation could be cleared. Northness and eastness were derived from aspect, measured at the carcass site.

	Ordinal day established	Average canopy	Distance to Pred cover	Profile A	Profile B	Profile C	Profile D	Profile E	Average profile
Ordinal day established	1.00	-0.20	0.18	-0.11	-0.10	-0.03	-0.06	-0.04	-0.08
Average canopy	-0.20	1.00	-0.49	0.63	0.66	0.66	0.62	0.30	0.66
Distance to Pred cover	0.18	-0.49	1.00	-0.39	-0.41	-0.42	-0.46	-0.39	-0.48
Profile A	-0.11	0.63	-0.39	1.00	0.99	0.91	0.74	0.34	0.91
Profile B	-0.10	0.66	-0.41	0.99	1.00	0.92	0.77	0.36	0.92
Profile C	-0.03	0.66	-0.42	0.91	0.92	1.00	0.88	0.42	0.94
Profile D	-0.06	0.62	-0.46	0.74	0.77	0.88	1.00	0.61	0.92
Profile E	-0.04	0.30	-0.39	0.34	0.36	0.42	0.61	1.00	0.64
Average profile	-0.08	0.66	-0.48	0.91	0.92	0.94	0.92	0.64	1.00
Actual Slope	0.04	0.04	-0.19	0.08	0.06	0.14	0.13	0.11	0.12
Actual Elevation	0.02	0.28	0.12	0.16	0.16	0.13	0.05	0.05	0.12
Average veg height	-0.20	0.82	-0.38	0.47	0.48	0.55	0.50	0.19	0.50
Distance paved road	-0.11	0.04	-0.10	0.16	0.17	0.13	0.20	0.19	0.20
Distance all road	-0.04	0.16	-0.29	0.16	0.19	0.17	0.13	0.10	0.17
Initial weight kg	-0.14	-0.08	-0.10	-0.06	-0.05	-0.12	-0.08	0.08	-0.05
Max Ascent	-0.29	0.76	-0.59	0.73	0.75	0.72	0.68	0.38	0.75
Min Ascent	-0.17	0.82	-0.45	0.57	0.59	0.67	0.62	0.29	0.63

Table A2 (cont.)

	Ordinal day established	Average canopy	Distance to Pred cover	Profile A	Profile B	Profile C	Profile D	Profile E	Average profile
Northness	-0.11	0.23	-0.26	0.19	0.18	0.20	0.17	0.08	0.19
Eastness	0.01	-0.10	0.10	-0.08	-0.10	-0.09	-0.04	-0.01	-0.07

Table A2 (cont.)

	Actual Slope	Actual Elevation	Average veg height	Distance paved road	Distance all road	Initial weight kg	Max Ascent	Min Ascent	Northness	Eastness
Ordinal day established	0.04	0.02	-0.20	-0.11	-0.04	-0.14	-0.29	-0.17	-0.11	0.01
Average canopy	0.04	0.28	0.82	0.04	0.16	-0.08	0.76	0.82	0.23	-0.10
Distance to Pred cover	-0.19	0.12	-0.38	-0.10	-0.29	-0.10	-0.59	-0.45	-0.26	0.10
Profile A	0.08	0.16	0.47	0.16	0.16	-0.06	0.73	0.57	0.19	-0.08
Profile B	0.06	0.16	0.48	0.17	0.19	-0.05	0.75	0.59	0.18	-0.10
Profile C	0.14	0.13	0.55	0.13	0.17	-0.12	0.72	0.67	0.20	-0.09
Profile D	0.13	0.05	0.50	0.20	0.13	-0.08	0.68	0.62	0.17	-0.04
Profile E	0.11	0.05	0.19	0.19	0.10	0.08	0.38	0.29	0.08	-0.01
Average profile	0.12	0.12	0.50	0.20	0.17	-0.05	0.75	0.63	0.19	-0.07
Actual Slope	1.00	-0.11	0.10	0.02	-0.07	0.30	0.15	0.27	-0.22	-0.15
Actual Elevation	-0.11	1.00	0.20	0.09	0.28	0.07	0.29	0.25	0.07	0.00
Average veg height	0.10	0.20	1.00	-0.12	0.09	-0.16	0.62	0.81	0.25	-0.06
Distance paved road	0.02	0.09	-0.12	1.00	0.23	-0.12	0.05	-0.02	-0.12	0.14
Distance all road	-0.07	0.28	0.09	0.23	1.00	-0.17	0.22	0.13	0.11	0.11
Initial weight kg	0.30	0.07	-0.16	-0.12	-0.17	1.00	0.12	-0.08	-0.14	-0.02
Max Ascent	0.15	0.29	0.62	0.05	0.22	0.12	1.00	0.75	0.26	-0.17
Min Ascent	0.27	0.25	0.81	-0.02	0.13	-0.08	0.75	1.00	0.27	-0.09
Northness	-0.22	0.07	0.25	-0.12	0.11	-0.14	0.26	0.27	1.00	0.11
Eastness	-0.15	0.00	-0.06	0.14	0.11	-0.02	-0.17	-0.09	0.11	1.00

Table A3. Logistic regression for condor presence relative to distance to paved roads when only natural mortalities are considered, Cedar Mountain, UT, May – September 2022, 2023.

Model: Condor presence ~ distance to paved road			
	Estimate	Std. Error	Pr(>|z|)
(Intercept)	-1.79	1.37	0.19
Distance paved road	0.005	0.003	0.054

APPENDIX B

CHAPTER III SUPPORTING INFORMATION

Table B1. Results of Tukey Honest Significant Difference test for proportion time spent vigilant across species pairs. P values were automatically adjusted for multiple comparisons.

	diff	lwr	upr	p adj
coyote-condor	-0.12	-0.39	0.16	0.93
domestic dog-condor	-0.06	-0.31	0.19	1.00
eagle-condor	0.00	-0.10	0.09	1.00
fox-condor	-0.07	-0.39	0.24	1.00
great horned owl-condor	0.25	-0.28	0.79	0.86
raven-condor	0.06	-0.04	0.16	0.63
skunk-condor	-0.30	-0.83	0.23	0.72
vulture-condor	0.10	0.02	0.19	0.01
domestic dog-coyote	0.06	-0.30	0.41	1.00
eagle-coyote	0.11	-0.16	0.38	0.93
fox-coyote	0.04	-0.36	0.45	1.00
great horned owl-coyote	0.37	-0.22	0.96	0.57
raven-coyote	0.18	-0.10	0.45	0.53
skunk-coyote	-0.18	-0.77	0.41	0.99
vulture-coyote	0.22	-0.05	0.48	0.20
eagle-domestic dog	0.05	-0.19	0.30	1.00
fox-domestic dog	-0.01	-0.40	0.37	1.00
great horned owl-domestic dog	0.31	-0.26	0.89	0.75
raven-domestic dog	0.12	-0.13	0.36	0.85
skunk-domestic dog	-0.24	-0.82	0.34	0.93
vulture-domestic dog	0.16	-0.08	0.40	0.46
fox-eagle	-0.07	-0.38	0.24	1.00
great horned owl-eagle	0.26	-0.27	0.79	0.84
raven-eagle	0.06	-0.02	0.15	0.31
skunk-eagle	-0.29	-0.82	0.24	0.73
vulture-eagle	0.11	0.04	0.17	0.00
great horned owl-fox	0.33	-0.28	0.94	0.76
raven-fox	0.13	-0.18	0.44	0.92
skunk-fox	-0.23	-0.83	0.38	0.97
vulture-fox	0.18	-0.13	0.48	0.69
raven-great horned owl	-0.20	-0.73	0.34	0.97
skunk-great horned owl	-0.55	-1.30	0.19	0.34
vulture-great horned owl	-0.15	-0.68	0.38	0.99
skunk-raven	-0.36	-0.89	0.17	0.47
vulture-raven	0.04	-0.03	0.11	0.58

Table B1 (cont.)

	diff	lwr	upr	p adj
vulture-skunk	0.40	-0.13	0.93	0.30

Table B2. Estimate, standard error, z value, and p value of non-competitive GLMMs for condor proportion of time spent vigilant on carcasses in Iron County, Utah, May-September 2022, 2023. Average vegetation height was the average of 15 measurements of tallest vegetation, taken each meter in a random direction from the carcass. Lowest section of understory cover is understory coverage from 0 – 0.5 m, from the carcass to 15 m away. Distance to predator cover is the nearest distance at which a board (0.9 m by 0.3 m) could be completely obscured. Distance to paved and all roads were digitally calculated using ArcGIS using road layers and GPS points of the carcass. Maximum group size is the maximum number of other individuals present either at the arrival or departure of the focal individual. Number of displacement is the summed number of displacements caused by an individual during its visit. Initial weight is the starting weight of the carcass when established, either weighed on site (<25 kg) or estimated from published accounts (>25 kg). Ordinal day established is the number of days since Jan 1st of that year that I established the carcass.

	Estimate	Standard error	z value	Pr(>|z|)
Average veg height	0.06	0.05	1.13	0.259
Lowest section of understory cover	-0.14	0.09	-1.60	0.109
Distance to predator cover	0.03	0.01	1.97	0.049
Actual slope	0.22	0.06	3.55	0.000
Distance to predator cover: Actual slope	-0.01	0.00	-2.96	0.003
Distance paved road	0.00	0.00	0.16	0.872
Distance all road	0.00	0.00	0.44	0.660
Max group	0.13	0.00	58.82	0.000
Number of displacements	-0.01	0.00	-10.68	0.000
Arrival weight kg	0.00	0.00	1.26	0.206
Ordinal day established	0.01	0.00	1.29	0.196

APPENDIX C

CHAPTER IV SUPPORTING INFORMATION

Table C1. Pairwise comparison of species' mean feeding times at carcasses on Cedar Mountain, Iron county, Utah, May – September 2022, 2023, using a Kruskal-Wallis test. Observed difference is compared to critical difference to determine significant differences in feeding times between each pair of species. Condor-raven, condor-vulture, and eagle-raven differences are significant.

	Observed difference	Critical difference	Statistically significant?
Condor-coyote	198.64	235.09	FALSE
Condor-domestic dog	223.48	205.66	TRUE
Condor-eagle	34.09	73.52	FALSE
Condor-fox	132.31	235.09	FALSE
Condor-great horned owl	213.98	398.80	FALSE
Condor-raven	126.05	74.08	TRUE
Condor-skunk	196.98	398.80	FALSE
Condor-vulture	75.62	64.01	TRUE
Coyote-domestic dog	24.83	301.33	FALSE
Coyote-eagle	164.56	232.18	FALSE
Coyote-fox	66.33	322.13	FALSE
Coyote-great horned owl	15.33	455.57	FALSE
Coyote-raven	72.60	232.35	FALSE
Coyote-skunk	1.67	455.57	FALSE
Coyote-vulture	123.03	229.34	FALSE
Domestic dog-eagle	189.39	202.32	FALSE
Domestic dog-fox	91.17	301.33	FALSE
Domestic dog-great horned owl	9.50	441.10	FALSE
Domestic dog-raven	97.43	202.53	FALSE
Domestic dog-skunk	26.50	441.10	FALSE
Domestic dog-vulture	147.86	199.07	FALSE
Eagle-fox	98.22	232.18	FALSE
Eagle-great horned owl	179.89	397.08	FALSE
Eagle-raven	91.96	64.23	TRUE
Eagle-skunk	162.89	397.08	FALSE
Eagle-vulture	41.53	52.30	FALSE
Fox-great horned owl	81.67	455.57	FALSE
Fox-raven	6.27	232.35	FALSE
Fox-skunk	64.67	455.57	FALSE
Fox-vulture	56.69	229.34	FALSE
Great horned owl-raven	87.93	397.19	FALSE
Great horned owl-skunk	17.00	557.95	FALSE

Table C1 (cont.)

	Observed difference	Critical difference	Statistically significant?
Great horned owl-vulture	138.36	395.43	FALSE
Raven-skunk	70.93	397.19	FALSE
Raven-vulture	50.43	53.08	FALSE
Skunk-vulture	121.36	395.43	FALSE