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Use and Partitioning of Riparian Corridors by Mammalian Carnivores in Rio Mora National Wildlife Refuge

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MS ENVIRONMENTAL BIOLOGY
CAPSTONE PROJECT

by

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CHAPTER 1. LITERATURE REVIEW

Mammalian Carnivore Assemblages Structured by the Effects of Interspecific Competition

Introduction

Most of the focus on management of wildlife populations for their conservation stems from the use of bottom-up practices for managing community structure. Evidence of top-down regulation suggests that it also plays an important role in structuring communities and must be seriously considered for conservation efforts (Linnel & Strand, 2000; Miller et al., 2001). An ecological community includes all populations of the different species that co-occur in a particular area and includes various trophic levels. Producers, carnivores, and decomposers are limited by the availability of resources. Organisms in these trophic levels must compete for resources amongst members of the same trophic level, whereas populations of herbivores are most often limited by predation (Hairston et al., 1960). Within these trophic levels guilds are formed– A guild is a subunit of a community comprised of populations that exploit resources in a similar way. Guilds structure communities through the differences in the density and distribution of interacting populations via both bottom-up and top-down mechanisms (Blondel, 2003).

Bottom-up control regulates populations when the energy of a system flows upwards through trophic levels and populations that occupy higher levels depend on the energy available from the lower trophic levels. Carnivore population numbers are controlled through prey availability and herbivore populations through the availability of plant biomass. This bottom-up view minimizes the ecological importance of carnivores in a system and can justify maintaining low carnivore population numbers or their complete extirpation as they provide no ecological benefits to the community (Miller et al., 2001).

Top-down management strategies focus on the effects that predators have on maintaining herbivore populations through predation, thereby reducing the pressure herbivores apply on local plant biomass. Top-down management has been largely ignored as a conservation and management strategy (Linnel & Strand, 2000; Miller et al., 2001). When top-down management strategies are used, the presence of a carnivore guild prevents a single prey species that is competitively superior from outcompeting and excluding other species in the community (Estes et al., 2001). Knowing the factors that structure carnivore assemblages are important for better management of wildlife populations in order to restore ecosystem functionality.

Intraguild interactions, more specifically through interspecific competition, provide the mechanisms by which density and distribution structure a mammalian carnivore assemblage (Wiens 1993). Interspecific competition can be *exploitative*, where a resource becomes limited once a species consumes said resource, it no longer can be used by other species (Linnel & Strand, 2000), or *interference*, where one species denies access and prevents the use of a resource by another potential competitor (Mumma et al. 2017). Exploitative interactions among predators are well documented and are similar to the same interactions among prey species (Linnel & Strand, 2000). Examples of exploitative interactions include predator-prey, host-pathogen, and brood parasitism interactions (Holt 2011). Most studies involving interspecific interactions have focused on exploitative interactions as drivers of community structure, but interference competition often plays a more important role in determining densities and distribution of species, two key factors in determining community structure (Case & Gilpin, 1974).

Interference competition can be further subdivided into two important interactions: *interspecific killing* (IK) and *intraguild predation* (IGP). Interspecific killing is the killing of an individual of a potentially competing species without any immediate energetic gain to the predator species (Polis et al. 1989). On the other hand, intraguild predation is defined as the killing and consuming of a potential competitor within the same guild. The effects of interference competition on the structure of assemblages within the order of Carnivora in the African and American continents will be the focus of this review. In areas where resources are low, carnivore assemblage structure is dictated by the effects of interspecific competition. Morphological and behavioral adaptations mitigate the pressures of intraguild competition. Specifically, mammalian carnivores partition resources in both space and time through differences in occupancy.

Interspecific Killing and Intraguild Predation

Interspecific killing and intraguild predation are common interactions among various African and American carnivore families. Estimates of IK for some species account for as much as 89% of total deaths in the victim population and a review of 599 potential intraguild predators and 763 potential intraguild prey across a taxonomic gradient found frequencies of IGP ranging from 58.4 to 86.7% (Arim & Marquet, 2004; Kamler et al., 2003). In South America, larger hypercarnivorous felids, jaguars (*Pantera onca*), pumas (*Puma concolor),* and ocelots (*Leopardus pardalis*) account for 80% of cases where they were identified as killers and smaller omnivorous families were more likely to become prey with procyonids and mephitids accounting for 51% of the victim species (de Oliveira & Perreira, 2013). In the African continent, carnivore assemblages are under the same pressures as those found in the American continent. Competition among conspecifics and other species as well as predation pressures occur in both continents.

Therefore, potential prey and potential killer carnivore families are similar across the two continents (Caro & Stoner, 2003).

IGP and IK may be symmetrical, where both interacting species can kill each other, or asymmetrical, where one species kills the other. The degree of symmetry depends on the age, size, and grouping. Smaller species may kill cubs, young, or subadult individuals of the larger species but in general, larger species usually kill both adult and juvenile individuals of the smaller species (Palomares & Caro, 1999). Grouping allows smaller species such as wolves (*Canis lupus*) to kill larger individuals such as black bears (*Ursus americanus*) (Rogers & Mech 1981; Paquet & Carbyn 1986). The benefits of IK and IGP also include the freeing of resources that otherwise would be used by a competitor that is killed. In addition to the benefits, IGP and IK provide an energetic resource when consuming the victim (Case & Gilpin, 1974). IGP and IK are influenced by a variety of factors, including the opportunity to eliminate a potential competitor, differences in body mass, degree of food overlap, food scarcity, and degree of phylogenetic overlap (Case & Gilpin, 1974; Donadio & Buskirk, 2006; Fedriani et al., 2000; Hass, 2009; Hunter & Caro, 2008). Competition theory suggests that a competitor should be eliminated when the benefits outweigh the cost of the interaction.

The frequency of attack depends on the difference in body mass between the two interacting species. When differences in mass are at the extremes of small and large, killings are less likely to occur. Intermediate differences in body mass result in more interspecific killing with aggressive interaction reaching a maximum when the larger species is 2-5.4 times the mass of the victim species with grouping species killing larger victims than solitary species (Donadio & Buskirk, 2006, Palomares & Caro, 1999).

In many cases, dietary overlap may lead to aggressive interactions between carnivore species. In North America, pumas (*Puma concolor*) steal kills from bobcats (*Lynx rufus*), potentially killing them in the process (Hass, 2009). Extensive dietary overlap among large African carnivores is correlated with high levels of interspecific aggression among them (Mills & Biggs, 1993). Many examples of larger predators stealing kills and killing competitors in the African continent exist as well. Most notably, cheetahs (*Acinonyx jubatus*) lose their kill frequently to larger predators such as lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) and may be killed in the process (Durant, 1998).

Food overlap plays an important role in determining an aggressive interaction among predators as they are essentially competing for the same resource, but on the other hand, even if the degree of food overlap is high, when a potential competitor has a very similar body size, launching an attack carries a higher risk of injury, and fighting tends to be avoided even if the potential benefits of freeing an important resource are large (Donadio & Buskirk 2006).

Phylogenetic overlap between carnivore species also influences the degree of IGP and IK. Carnivore families tend to interact more with species in the same family than with species from different families (Donadio & Buskirk, 2006). A study of forty native South American mammalian terrestrial carnivore species describes the likelihood of each family overlapping and competing with another family through shared common attributes that may predispose them to IGP and IK (Hunter & Caro, 2008). Members of omnivorous families such as Ursidae and Canidae occur with a greater proportion of potential competitors than other members of carnivore families with more specialized diets such as members of the Felidae family (Hunter & Caro, 2008). Interactions and consumption of the victim species appear more common when food is scarce or contested (Palomares & Caro, 1999). As expected, the pressure of resource scarcity can lead to an increase in aggressive interactions between carnivore species.

With such a marked effect on possible competitors, IK and IGP may structure communities not only by reducing population numbers, but also by changing the behavior of potential competitors to avoid certain areas (Hass, 2009). The effects of IK and IGP include reduced population sizes or even extirpation of local carnivore species, and altered habitat use by a more subordinate species (Palomares and Caro, 1999, Mumma et al., 2017). IK and IGP decrease population size and growth rate of populations by directly increasing mortality rates (Linnell & Strand, 2000). This effect on population numbers shows that carnivores not only influence the community composition of their prey, but they may also impact the density and distribution of other carnivores, possibly changing the community structure (de Oliveira & Perreira, 2013).

The effect of body size on the distribution of some carnivore species can be seen at a local level as well as at a continental scale (Fedriani et al., 2000; Newsome & Ripple, 2015). In the Americas, studies have compared distribution and habitat use of large-sized, coyotes (*Canis latrans*), medium-sized, bobcats (*Lynx rufus*), and smaller-sized carnivores, grey foxes (*Urocyon cinereoargenteus*). Smaller carnivores were more likely to use different habitat than that used by the larger more dominant coyotes. Medium sized carnivores do not display avoidance behavior, using their habitat in equal proportions (Fedriani et al., 2000).

The same effects of IGP and IK on carnivore populations can be found when viewed at a continental scale and cascading effects on densities and distribution patterns become easier to determine. Coyote and red fox (*Vulpes vulpes*) densities and distributions are tied to the presence and distribution of wolf populations. Where wolves are absent due to extirpation, coyotes outnumber foxes in terms of population size, and where wolves are present, foxes outnumbered the coyote population in those areas (Newsome & Ripple, 2015). Some suitable habitats cannot be used by some carnivore species and thus, that species occurs at lower densities when co-occurring with other dominant species (Durant, 1998; Linnell & Strand, 2000).

The inability to use suitable habitat can also be seen in the African continent. Cheetahs exemplify the effects of IK and IGP on density and distribution. Cheetahs make use of competition refuges where their interspecific predators such as lions, hyenas, and leopards (*Panthera pardus*) occur less frequently, and so the dangers of IK and IGP are reduced (Durant, 1998). However, prey densities are also lower, resulting in a reduction of the carrying capacity of the refuges. Consequently, cheetahs can only survive in these refuges at much lower population densities (Durant, 1998; Linnell & Strand, 2000).

Adaptations

Many carnivores have adapted to the pressures of interspecific competition in order to minimize the effects of IGP and IK. Adaptations such as avoidance behaviors through spatiotemporal partitioning help reduce unfavorable encounters among mammalian carnivores. In case of an encounter, morphological adaptations, notably, differences in body mass, dentition, and body coloration help to resolve negative interactions.

In order to avoid IGP and IK, victim species may alter their use of space, known as a landscape of fear effect (Palomares & Caro, 1999). The best example of avoidance occurring in African carnivore families is that of cheetahs exhibiting local avoidance behavior when dealing with lions and hyenas as competitors. Although cheetahs always lose to direct competition, it is their use of competition refuges that allows their populations to persist (Durant, 1998).

Such effects and adaptations also occur in in North and South America, where bears have a preference for intermediate elevations and use a higher proportion of wetlands and forests, intermediate levels of open habitats, and lower amounts of conifer scrub. Other members of the local carnivore assemblage select for different habitat types that tend not to overlap with that of bears. Foxes tend to select higher elevations and lynx and coyotes select for lower elevations. Foxes use the highest proportion of wetlands and least proportion of open habitat. Coyotes use a higher proportion of open habitat than their co-occurring carnivore families and lynx use the higher proportions of conifer scrub and forest habitat (Mumma et al., 2017). At a finer scale, members of the Procyonidae and Mustelidae families may reduce competition from canids, felids, and ursids by being arboreal with the added effect of mustelids also being aquatic (Hunter & Caro, 2008).

The use of time partitioning as a tool to mediate conflict between the carnivore community is a well-established (Linnel & Strand, 2000, Edwards et al., 2015, Durant, 1998). The difference in circadian patterns from diurnal and nocturnal species creates a buffer effect on activity overlap. This effect is clearly seen when lions hunt mainly at night while African wild dogs (*Lycaon pictus*) hunt in the early morning and cheetahs around midday (Fedriani et al., 2000, Mills & Biggs, 1993). When resources are limited and spatially fixed, spatial partitioning may play a minor role compared to temporal partitioning for that resource. Temporal partitioning then becomes the main driver for coexistence among a large number of sympatric carnivore species, maintaining biodiversity (Edwards et al., 2015, Linnel & Strand, 2000).

Aside from behavioral adaptations to mediate interspecific competition, morphological adaptations also facilitate coexistence or enhance competition. Tooth morphology more adapted to killing and consuming of vertebrate prey may provide an advantage when faced with an interspecific fight with another species because they have the weaponry to succeed. On the other hand, less equipped carnivores attempt to avoid such interactions, signaling an interaction between morphological features and behavior (Case & Gilpin 1974, Donadio & Buskirk, 2006).

Apart from dental morphology, body morphology in the form of increased body mass and coloration can confer an advantage to carnivores faced with the pressures of IGP and IK. A greater degree of spatial partitioning in African carnivore species is often observed from the difference in body mass. Interactions among species pairs with larger differences in body mass showed the greatest degree of partitioning (Edwards et al., 2015). Species with a larger body mass as adults, pose an advantage in aggressive interactions by outgrowing potential predators and placing them in a competitive size refuge. This means their mass is large enough that they experience less instances of IK and IGP (Palomares & Caro, 1999; Woodward & Hilldrew, 2002). Bears are a prime example of species in a competitive size refuge and only in the case of brown bears (*Ursus arctos)* killing black bears, has a solitary carnivore been recorded as killing a potentially heavier carnivore (Palomares & Caro, 1999).

Coloration is also an important adaptation to mediate the pressure of interspecific competition. Conspicuous species with contrasting body and face coloration occur in areas with more potential predators than do species with less striking body coloration. Members of the family Mephitidae which include skunks advertise their noxious secretions with their aposematic coloration (Hunter & Caro, 2008), suggesting that IGP and IK are drivers for contrasting coat coloration.

Conservation & Conclusion

Throughout this review, the importance of interspecific competition has been discussed in the context of structuring carnivore assemblages locally, regionally, and at a continental scale.

The effects of IGP and IK have been found to be non-random (de Oliveira & Perreira, 2013, Donadio & Buskirk, 2006) and is determined in part by differences in body mass, degree of carnivory and food overlap, and competitive advantage. Adaptations, both morphological and behavioral may reduce the effects of IGP and IK. Avoidance behaviors drive a species to reduce its range or avoid their preferred habitat patches completely in the presence of a more dominant competitor. This shift may incur a reduction in carrying capacity due to less than favorable conditions and so the victim species may only be able to persist at lower densities. This is important when taking into account conservation efforts adapted for mammalian carnivores, such as reintroductions or population increase. IGP and IK also slow population growth for some carnivore species through changing mortality rates and decreased foraging efficiency (Linnell & Strand, 2000).

IGP and IK may cause one species to employ avoidance behaviors and change their use of habitat because of the presence of another carnivore species. This behavior places the affected species in a habitat with a reduced carrying capacity due to lower densities of prey or decreased habitat quality, therefore the species may only survive at a reduced density (Linnel & Strand, 2000). A complete understanding of these interactions is needed in order to fully understand the conditions in which conservation efforts must take place.

In the past, conservation efforts have mostly focused on bottom-up management, and studies on top-down effects have focused mainly on the relationship between carnivores and their prey species as well as the relationship between prey species and their habitat. Current management practices address the symptoms of an unbalanced system when viewed only through the lens of bottom-up management strategies. Top-down control practices have to be used as well in order to manage populations of predators and prey in ways that more closely resemble their natural states (Miller et al., 2001). If top-down effects are to be maintained alongside bottom-up effects, equal emphasis must be placed on the effects that mammalian carnivores have on co-occuring populations (Linnel & Strand, 2000). Interference competition among mammalian carnivore species differs from those between prey species in that they can change the demographics of an assemblage (Polis et al., 1989).

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CHAPTER 2. GRANT PROPPOSAL

Use of Restored vs Unrestored Riparian Corridors by Mammals in Rio Mora National Wildlife Refuge

Abstract

Drought conditions and land conversion across the Southwestern U.S. for agricultural and livestock use have led to a cascade of effects that lowers ecosystem functionality in terms of providing adequate habitat for wildlife. Early signs of lowered functionality include the formation and expansion of arroyos, steep-sided gullies formed by fast-flowing water. Arroyo restoration efforts aim to restore ecological function by decreasing the degree of soil erosion. When restoration decreases erosion, downstream riparian habitat typically improves because water speed and therefore river channelization is reduced. These restored streams serve as corridors for wildlife movement because they house more permanent water resources that wildlife use. Rio Mora National Wildlife Refuge (RMNWR) has undertaken several efforts to restore several arroyos, however the extent to which mammals prefer restored over unrestored riparian corridors, and how habitat quality influences mammalian density in those corridors is unknown. Furthermore, the degree to which mammals partition resources through space and time in these corridors is also unknown. Therefore, I will analyze existing camera trap data to quantify mammal occupancy in both restored and unrestored corridors and conduct field surveys to measure habitat quality. Then, using statistical models, I will assess how habitat characteristics distinguish and influence mammalian occupancy in each corridor type. Lastly, using the extensive photographic record, I will test whether mammals partition their use of corridors in order to reduce competition. The information collected and analyzed as part of this project will

not only communicate the success of restoration efforts at RMNWR, but also elucidate mechanisms by which competition among mammals is mitigated to ensure coexistence.

Project Description

Background/Rationale/Significance

Riparian corridors have long been accepted as important hot spots of biodiversity because they connect fragmented landscapes to allow wildlife to more easily migrate or disperse between habitat patches of varying quality (Clements et al., 2011; Gillies & St. Clair, 2008; Hilty et al., 2006; Walter et al., 2011). Humans degrade riparian corridors when soil water absorption upstream is decreased by changing natural grasslands into rangeland for livestock, and when surrounding rivers are diverted for crop irrigation. By increasing the water's erosive potential, water diversions impair the ecosystem services provided by the corridor. Erosion increases water speed and lowers the water table, resulting in a loss of riparian vegetation. The newly denuded landscape suffers from a loss in biodiversity because the formerly complex habitat is notably simplifed (Noss & Daly, 2006; Wissmar & Beschta, 1998).

Arroyo formation and soil erosion are serious problems in the Southwestern U.S. and Rio Mora National Wildlife Refuge (RMNWR) serves as a good example of the effects of soil erosion on downstream riparian habitat in a semi-arid ecosystem. The refuge is located in a semi-arid matrix of canyons, piñon-juniper forest, ponderosa pine woodlands, and short-grass prairie where access to water is limited to riparian corridors. Historically, heavy cattle grazing and drought reduced the local vegetation and impaired the soil's ability to retain water. The resulting increase in run-off and erosion created arroyos that further enhanced the erosive potential of water, leading to a positive feedback that further exacerbates arroyo formation (Zeedyk and Jansens, 2004). RMNWR has undertaken restoration efforts in order to combat the formation of arroyos and decrease the downstream effects of soil erosion by installing one-rock dams that help retain water for longer periods of time. An important consequence of such arroyo restoration efforts is the creation of wetlands in the canyons and improvement in riparian vegetation status. Riparian vegetation regulates stream temperatures by increasing shade, sequesters sediment and nutrients, stabilizes the riverbank, and provides cover and protection from predators to prey species (Richardson et al., 2007). Riparian vegetation also provides food for herbivores, and by attracting prey, carnivores.

Predatory mammals can influence ecological community structure directly by consuming prey, and indirectly by altering prey behavior through fear-driven responses (Ripple & Beschta 2004). Because mammalian carnivores control herbivore populations through predation, they reduce the grazing pressure herbivores apply to local plant biomass. Consequently, when apex predators are lost from an ecosystem, the resulting trophic cascade that occurs leads to the overpopulation of certain species and a reduction of biodiversity (Miller et al., 2001). On the other hand, mammalian carnivores also interact with each other when moving through corridors or when searching for resources. These interactions lead to intraguild predation (i.e., killing and consumption of other mammalian carnivores) and interspecific killing (i.e., killing of other mammalian carnivores due to competition) (Linnel & Strand, 2000; Palomares & Caro, 1999). In order to avoid negative intraguild interactions, mammalian carnivores may either avoid areas inhabited by other carnivores (i.e., space partitioning) or only visit those areas at times when another carnivore is absent (i.e., temporal partitioning) (Palomares & Caro, 1999).

Mammals partition resources in order to avoid competition with other carnivore species (Linnel & Strand, 2000, Edwards et al., 2015). When resources are scarce and spatially fixed, spatial partitioning for that resource plays a minor role compared to temporal partitioning. Thus, temporal partitioning allows a large number of co-occurring carnivore species to coexist, thereby setting a template for high biodiversity (Edwards et al., 2015, Linnel & Strand, 2000).

The use of riparian corridors varies among mammalian species that show a preference for certain corridor traits. For example, mammalian carnivores such as mountain lions (*Puma concolor*) and bobcats (*Lynx rufus*) favor wide corridors with brush and dense understory. Skunks (*Mephitis mephitis*) and coyotes (*Canis latrans*) typically prefer young or edge habitat with open canopy, and raccoons (*Procyon lotor*) favor easy access to trees and water (Derugin et al., 2015; Dickson et al., 2005; Hilty & Merlander, 2004).

Despite the value of riparian corridors to local terrestrial fauna, few studies have examined the response of medium and large-sized mammals to restoration efforts that seek to improve or create functional corridors within a fragmented landscape (Derugin et al., 2015). One such study was conducted along the Sacramento River National Wildlife Reserve, CA, where riparian habitat was restored, abundances of large and medium-sized mammals was observed to increase during the early successional stages (Derugin et al., 2015). Furthermore, one of the greatest challenges of riparian corridor restoration is predicting when the restored corridor will be colonized by local fauna. Such prediction allows restoration practitioners to assess the progress of restoration goals (Derugin et al., 2015). In order to determine if riparian corridor restoration efforts at RMNWR have created functional habitat for mammals, the occupancy of restored vs unrestored riparian corridors by mammals must be quantified and compared. Furthermore, the extent that improved mammalian habitat may result in increased competition for those resources is also unknown.

The report generated by this research effort will assess whether restoration efforts have improved mammalian habitat at RMNWR. The refuge can then communicate these empirical results to surrounding landowners. The results and protocol developed here can also be used as a model for conservation and management of other mammal species occurring in semi-arid ecosystems indicative of the American Southwest. This project aligns with the mission of Regis University by expanding on the idea of restoring ecosystem processes in order to make a positive impact in a changing society. The results of this project will help inform communities on how to strike a balance between their needs and preserving and restoring important ecosystem services for their community and future generations.

Purpose and Specific Aims, Questions and Hypotheses

The objectives of this study are a) to compare the extent to which mammals occupy restored and unrestored corridors at RMNWR), b) to assess whether differences in habitat characteristics between corridors drive differences in mammalian occupancy, and c) to understand the mechanisms by which mammals partition their use of corridors.

Question 1: *How does habitat quality differ in restored and unrestored riparian corridors at RMNWR?*

Hypothesis & Prediction 1: Unrestored riparian corridors are subject to the cascading effects of unmitigated upstream soil erosion, and therefore functional riparian habitat is reduced. Restored riparian corridors retain more water resulting in a more abundant and diverse plant community than in unrestored corridors.

Question 2: *How does mammal occupancy in restored riparian corridors differ from occupancy in unrestored corridors at RMNWR, and does this difference correlate with differences in habitat quality?*

Hypothesis & Prediction 2: Restored corridors provide a more functional habitat for mammals by providing food, water, and protection for herbivores and an increase in prey density that attracts mammalian predators. If habitat quality is greater in restored corridors, then mammals will be observed more frequently in restored compared to unrestored corridors.

Question 3: *How do different species within the mammalian carnivore assemblage spatiotemporally partition the use of restored and unrestored riparian corridors at Rio Mora NWR?*

Hypothesis & Prediction 3: Mammalian carnivores are under high pressures of interspecific competition since resources, such as water and prey are limited at RMNWR. Carnivores will partition the use of riparian corridors spatiotemporally in order to avoid conflict with other species. If limiting resources compound the effects of competition, and restored corridors provide more resources, then a greater degree of mammalian spatiotemporal partitioning will be observed at unrestored corridors compared to restored corridors. On the other hand, the presence of improved habitat in restored corridors may trigger more intense competition among carnivores, resulting in more notable partitioning at those sites.

Methods

To answer these questions, I will integrate data collected from habitat surveys near camera traps that have recorded mammalian presence since 2016 (Figure 1). These camera traps are a set of cameras deployed to be able to study wildlife unobtrusively. A set of 30 Bushnell CAM HD Essential (Model: 119736C) camera traps were deployed at the sites. The cameras were set to take a photograph at 10 second intervals when detecting movement within a range of 36ft-100ft. The species I expect to observe more commonly in the location of the camera traps include: skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), coyotes (*Canis latrans*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), mountain lions (*Puma concolor*), and mule deer

(*Odocoileus hemionus*).

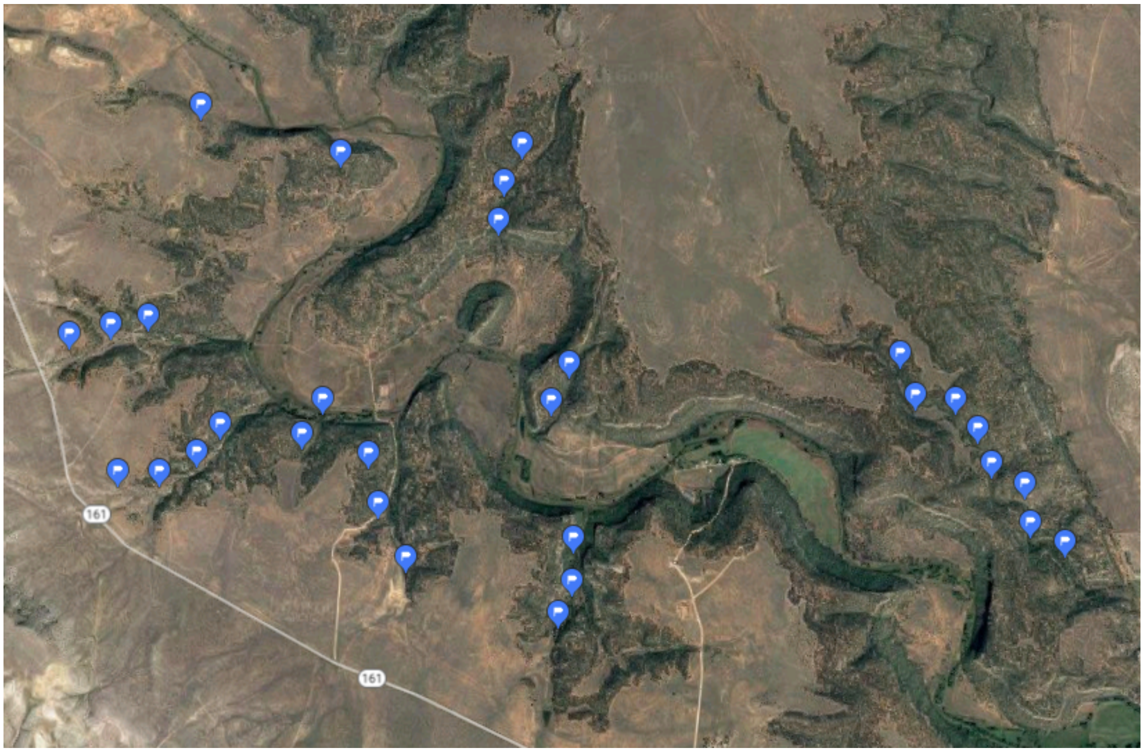

Figure 1: Location of the 30 camera traps across restored and unrestored study sites at Rio Mora National Wildlife Reserve, NM

Q1: ***How does habitat quality differ in restored and unrestored riparian corridors at RMNWR?***

In July 2019, to quantify habitat factors that differ between restored and unrestored riparian corridors, habitat assessments will be performed every 50m along a 500m transect that runs parallel to the watercourse and is centered on each camera trap (Figure 1). Based on the protocol of Santos et al., (2011), I will estimate overstory (> 1.5m) and understory (<1.5m) density as scarce or dense, depending on whether large gaps (>10 m) between plants occur along >50% of the transect (scarce) or the vegetation is a continuous patch (dense). Plant richness and percent composition of grasses, forbs, and other wetland plants will be estimated at these positions as well. I will measure overstory canopy cover on both riverbanks every 50m while standing 5m from the bank, facing upstream, downstream, toward bank, and away from bank. Water availability will be measured by recording water depth and water width at the beginning and end of each 50m segment.

Q2: How does mammalian occupancy of restored riparian corridors differ from use of unrestored corridors?

A randomized subset of the complete photograph data set will be analyzed by Regis University Environmental Biology graduate students to identify the mammalian species present in the photographs. Students will be trained to identify known local mammal species using a species list and photographs. These coded photographs will then be used to train a machine learning algorithm developed by Norouzzadeh et al., (2017). Machine learning algorithms find and recognize specific patterns in photographs coded by the investigator, and then apply those patterns to identify the objects in unknown photographs. These algorithms identified animals in an African wildlife reserve to species with greater than 93.8% accuracy. To test if the algorithm correctly identifies the presence or absence of local mammals, a subset of random photographs will be verified by graduate students once more. A spatially explicit capture–recapture model (SECR) will be used to estimate density and compare mammalian species richness at each site using a Bayesian approach. SECR models combine information on capture locations and the organism's capture probability to estimate density (Foster & Harmsen, 2012).

Q3: How does mammalian spatiotemporal partitioning of the restored corridors differ from that of the unrestored corridors?

The extent of temporal partitioning at restored and unrestored camera trap sites will be calculated by comparing the time stamps from each photograph where the species is observed. Degree of time overlap will be analyzed using the camera detections. Activity patterns for each species will be estimated using kernel density estimation with the "*overlap*" package in R. Overlap for all species pairs will be calculated using the *coefficient of overlap*. The coefficient ranges from 0 (no overlap) to 1 (complete overlap) (Wang et al., 2016). To examine spatial partitioning between species at camera trap sites, the proportion of independent events at each site will be calculated for each species. A heat-map of the sites will be generated using R to quantify the regions used most frequently by each species. Then the extent of co-occurrence will be quantified using a linear model approach in R (Wang et al., 2016).

Project Requirements, Logistics, Timeline, and Negative Impacts

I have coordinated with RMNWR and obtained permission both to use the photographic data they have already generated and to conduct habitat surveys on RMNWR property. I will submit a supplemental map detailing the location of the camera traps and study sites for habitat surveys before sampling is to take place. Since I will not be catching or handling any animals, there is limited impact on local wildlife. Habitat surveys and riparian zone structure recordings will represent minimal impact to RMNWR lands.

Work Plan

Date	Activity	Deliverable
June 2019 - July 2019	● Obtain photographic data ● Coordinate sampling locations with RMNWR ● Conduct habitat surveys	● Raw data set of photographs ● Students able to identify local mammals to species
August 2019- Sep 2019	● Train machine learning algorithm ● Verify ML outputs	● Accuracy test of ML algorithm ● Results summary from ML algorithm
Oct 2019- Nov 2019	● Train students for photo analysis	● Occupancy analysis ● Spatiotemporal partitioning analysis

Dec 2019- Jan 2019	● Data analysis on ML outputs ● Spatiotemporal partitioning analysis ● Data analysis on habitat surveys	● Raw data habitat survey
Feb 2020- Mar 2020	● Begin report writing	● Data analysis on habitat
Apr 2020- May 2020	● Finish Draft reporting ● Finish report writing	● Draft report ● Final report

Relation to coursework/career goals

I am currently an Environmental Biology graduate student with a strong interest in mammalian carnivores and the interactions among them. This research study will allow me to implement the knowledge and skills I have learned in my time in the program. This study will further my education and career goals by allowing me to gain meaningful research experience that I can apply when continuing my education with a doctoral degree.

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CHAPTER 3. JOURNAL MANUSCRIPT

Use and Partitioning of Riparian Corridors by Mammalian Carnivores in Rio Mora National Wildlife Refuge

Abstract

Land conversion across the Southwestern U.S. for agricultural and livestock use and prolonged drought conditions cascade to reduce ecosystem function, including habitat provision for wildlife. Arroyo restoration efforts aim to improve wildlife habitat by decreasing soil erosion and enhancing water retention. These hydrologic and geomorphic changes increase the likelihood that wildlife use restored corridors by increasing riparian vegetation cover. Rio Mora National Wildlife Refuge (RMNWR) has restored several arroyos by installing a system of one-rock dams throughout the refuge, but the extent to which mammals prefer restored over unrestored riparian corridors and how habitat structure influences mammalian use and density in those corridors is unknown. To test whether arroyo restoration improves habitat for large mammals, we collected data on corridor morphology and vegetation structure in the vicinity of 30 camera traps along 10 corridors within the RMNWR. Habitat variability across camera traps was driven by corridor level differences in water availability, vegetation composition, and morphology, rather than restoration status. A total of fifteen species were recorded using two of the ten canyons. Mean species abundance differed only for three species that were found in one canyon versus another, while mean species occurrence showed a greater difference for nine of the fifteen species. Habitat structure effects tended to relate modestly to visitation rates.

Introduction

Riparian corridors have long been accepted as important hotspots of biodiversity because they connect fragmented landscapes, allowing wildlife to more easily migrate or disperse between habitat patches of varying quality (Clements et al., 2011; Gillies & St. Clair, 2008; Hilty et al., 2006; Walter et al., 2011). One of the main ways humans degrade riparian corridors is converting nearby land to rangeland or agriculture and re-engineering natural water flows for the purpose of irrigation (Poff et al., 1997; Schottler et al., 2014). When rivers are diverted or channelized to provide irrigation water, water moves more quickly through the system thereby lowering the water table. These hydrological changes result in degradation or loss of in-corridor riparian vegetation as well as vegetation located in the floodplain (Schottler et al., 2014; Zeedyk & Jansens, 2004). The newly denuded landscape suffers from a loss of biodiversity because the formerly complex habitat is notably simplified (Noss & Daly, 2006; Wissmar & Beschta, 1998).

Arroyo formation and soil erosion are serious problems in the Southwestern U.S. and Rio Mora National Wildlife Refuge (RMNWR) serves as a good example of the effects of soil erosion on downstream riparian habitat in a semi-arid ecosystem. The refuge is located in a semi-arid matrix of canyons, piñon-juniper forest, ponderosa pine woodlands, and short-grass prairie where access to water is limited to riparian corridors. Historically, heavy cattle grazing and drought reduced vegetation and compacted the soil, impairing its ability to retain water. The resulting increase in run-off and erosion further enhanced the erosive potential of water, leading to a positive feedback loop that exacerbated arroyo formation (Zeedyk & Jansens, 2004). To combat the formation of arroyos and decrease the downstream effects of soil erosion, RMNWR has aimed to retain water and soil in upstream canyons by installing one-rock dams. An important consequence of such arroyo restoration efforts is the creation of wetlands in the canyons and improvement in riparian vegetation quantity and quality. Riparian vegetation regulates stream temperatures by increasing shade, sequesters sediment and nutrients, stabilizes the riverbank, and provides cover and protection to native fauna (Richardson et al., 2007). Riparian vegetation also provides food for herbivores, and by attracting prey, carnivores.

Predatory mammals can influence ecological community structure through top-down control directly by consuming prey, and indirectly by altering prey behavior through fear-driven responses (Ripple & Beschta 2004). Because mammalian carnivores control herbivore populations through predation, they reduce the grazing pressure herbivores apply to local plant biomass. Consequently, when apex predators are lost from an ecosystem, the resulting trophic cascade that occurs leads to the overpopulation of certain species and a reduction of biodiversity (Miller et al., 2001). On the other hand, mammalian carnivores also interact with each other when moving through corridors or when searching for resources. These interactions may lead to interference competition by which intraguild predation (i.e., killing and consumption of other mammalian carnivores) and interspecific killing (i.e., killing of other mammalian carnivores due to competition) are the main mechanisms (Linnell & Strand, 2000; Palomares & Caro, 1999).

In order to avoid negative intraguild interactions, mammalian carnivores may either avoid areas inhabited by other carnivores altogether (i.e., spatial partitioning) or only visit those areas at times when another carnivore species is absent (i.e., temporal partitioning) (Palomares & Caro, 1999). Mammals partition resources in order to avoid competition with other carnivore species (Linnell & Strand, 2000, Edwards et al., 2015). When resources are scarce and spatially fixed, spatial partitioning for that resource plays a minor role when compared to temporal partitioning. Thus, temporal partitioning allows for a large number of co-occurring carnivore species to coexist, thereby setting a template for high biodiversity (Edwards et al., 2015, Linnell

& Strand, 2000). Spatial and temporal partitioning are best illustrated by carnivore communities in Africa, where water resources are limited and spatially fixed. Edwards et al. (2015) demonstrated that carnivore communities could more easily reduce competition and co-occur around spatially fixed water sources in commercial farms in Namibia when they visited these resources at different times.

Habitat structure and species behavior interact to influence habitat use by mammalian communities (Ruth & Murphy 2010; Atwood et al. 2011; Wang et al., 2015). For example, mammalian carnivores that are ambush predators such as mountain lions (*Puma concolor*) and bobcats (*Lynx rufus*) favor wide corridors with brush and dense understory for cover. Cursorial predators such as striped skunks (*Mephitis spp.*), spotted skunks (*Spilogale spp.*), and coyotes (*Canis latrans*) typically prefer young or edge habitat with open canopy, and raccoons (*Procyon lotor*) favor easy access to trees and water (Derugin et al., 2015; Dickson et al., 2005; Hilty & Merlender, 2004). On the other hand, up to 92% of gray fox (*Urocyon cinereoargenteus*) mortality is attributed to coyotes (Farias et al., 2005), so they tend to avoid edge and more open habitats and exhibit greater nocturnal activity (Fedriani et al., 2000; Wang et al., 2015). As large, omnivorous predators, black bear (*Ursus americanus)* habitat use is mainly influenced by the distribution and abundance of resources (Moyer et al., 2007; Garshelis & Pelton, 1981; Koehler & Pierce, 2003; Jonkel & Cowan, 1971; Lindzey & Meslow, 1977) that include oak (*Quercus sp.*) mast, salmon (*Oncorhynchus sp.*), berry crops, ants (*Formica sp.*), and young ungulates (Ostfeld et al., 1996; Grosse et al., 2003; Gende et al., 2004; Liebhold et al., 2004; Garneau et al., 2008; Rayl et al., 2015).

Mammalian carnivore occupancy studies in the arid Southwest have found that occupancy is controlled by a combination of biotic and abiotic factors (Bender et al., 2017;

Derugin et al., 2015), but the degree to which that occupancy is spatially or temporally partitioned is poorly understood (Ruth & Murphy, 2010). Carnivore presence in the San Andres Mountains of southcentral New Mexico was more so controlled by habitat structure and prey availability than occupancy of any other carnivores (Bender et al., 2017). The authors observed that mountain lion occupancy was mostly influenced by proximity to water, coyote occupancy was influenced by terrain ruggedness and presence of primarily lagomorph prey, and bobcat occupancy was influenced primarily by small prey and proximity to water (Bender et al., 2017). The goal of restoration is to provide suitable habitat for animal communities to occupy but despite the value of riparian corridors to local terrestrial fauna, few studies have examined the response of medium and large-sized mammals to restoration efforts that seek to improve or create functional corridors within a fragmented landscape (Derugin et al., 2015). After riparian habitat was restored within the Sacramento River National Wildlife Reserve, CA, abundances of large and medium-sized mammals increased during the early successional stages (Derugin et al., 2015). Despite the improvements observed in mammalian communities, predicting when the restored corridor will be colonized by local fauna remains a challenge. Such prediction allows restoration practitioners and wildlife managers to assess the progress of restoration goals (Derugin et al., 2015).

In order to determine if riparian corridor restoration efforts at RMNWR have created functional habitat for mammals, mammalian occupancy of restored and unrestored riparian corridors must be quantified and compared. In order to assess whether restoration has improved habitat for mammalian carnivores and their prey, I measured habitat features along the corridors of RMNWR and compared them to the observed animal community occupying these corridors. By increasing the residence time of water in arroyos, restoration efforts should result in more suitable habitat in restored canyons when compared to unrestored canyons. I predict that this increase in resources will result in higher occupancy and abundance of mammalian carnivores and their prey at restored canyons.

Methods

Study Site

Rio Mora National Wildlife Refuge encompasses 1,709 hectares of the 121,406-hectare Rio Mora Watershed Conservation Area (Figure 1). The refuge consists primarily of semi-arid shortgrass prairie and includes a matrix of canyons through which roughly 8 kilometers of the Rio Mora river flows. The refuge is punctuated with piñon-juniper and ponderosa pine woodlands that stretch throughout the canyons and provide perennial and ephemeral seeps, springs, and ponds. The riparian corridors formed by these canyons at RMNWR serve as important resource hotspots as well as corridors for wildlife movement. Because of the importance of these canyons, managers at the refuge initiated a restoration program of one-rock dam installations. These small rock structures attempt to prevent arroyo degradation by slowing the speed of water and reducing erosion.

To quantify the environmental characteristics that underlie mammalian occupancy as well as to determine the effects of restoration efforts along these corridors, I measured corridor morphology, vegetation cover, and vegetation density within corridors and along the adjacent riparian zones. In order to capture and compare mammalian occupancy to environmental characteristics, thirty camera traps in total were deployed along these corridors. Half of the cameras were placed in restored corridors, while the other fifteen were placed in unrestored corridors (Figure 1).

Corridor Morphology

To determine corridor morphology around each camera trap, I set up a 220-m long transect along the length of the corridor. The transects were divided into 20m plots with the cameras centered at plot zero for a total of 11 plots– 10 plots upstream of the camera site, 10 plots downstream, and the plot at the center containing the camera trap (Fig. 2).

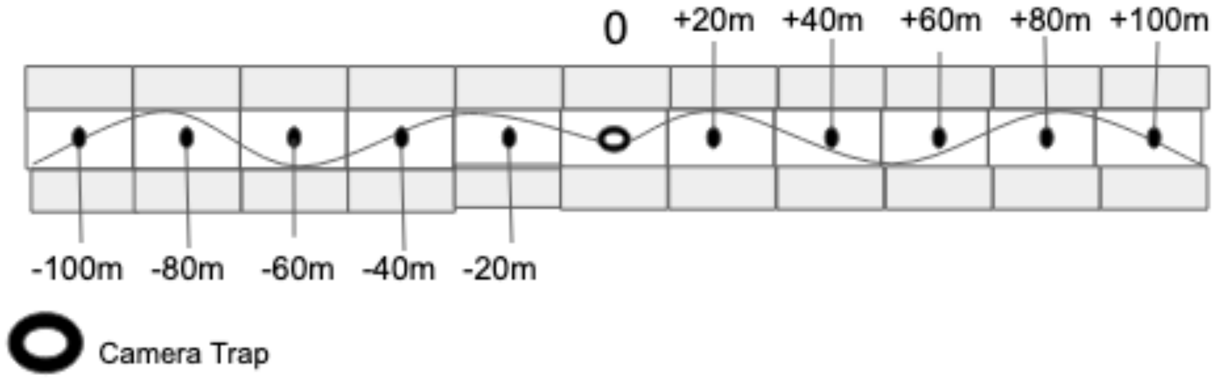


Figure 2: Transect set-up at every camera trap site for a total of 30 transects (15 unrestored, 15 restored). Vertical lines demarcate plot boundaries. Gray areas represent riparian zones.

Upstream plots were denoted by positive values (e.g. +20m, +40m, +60m, etc.) and downstream plots were denoted by negative values (e.g. -20m, -40m, -60m, etc.). At the center of each plot and wherever it was possible, I measured bottom corridor width, right and left bank heights, corridor bearing, presence/absence of standing water, and distance from the center of the plot to the nearest source of water. I also calculated the slope for each canyon using Google Earth Pro and assigned an accessibility score to each plot that would denote the degree of difficulty in perpendicularly accessing the corridor.

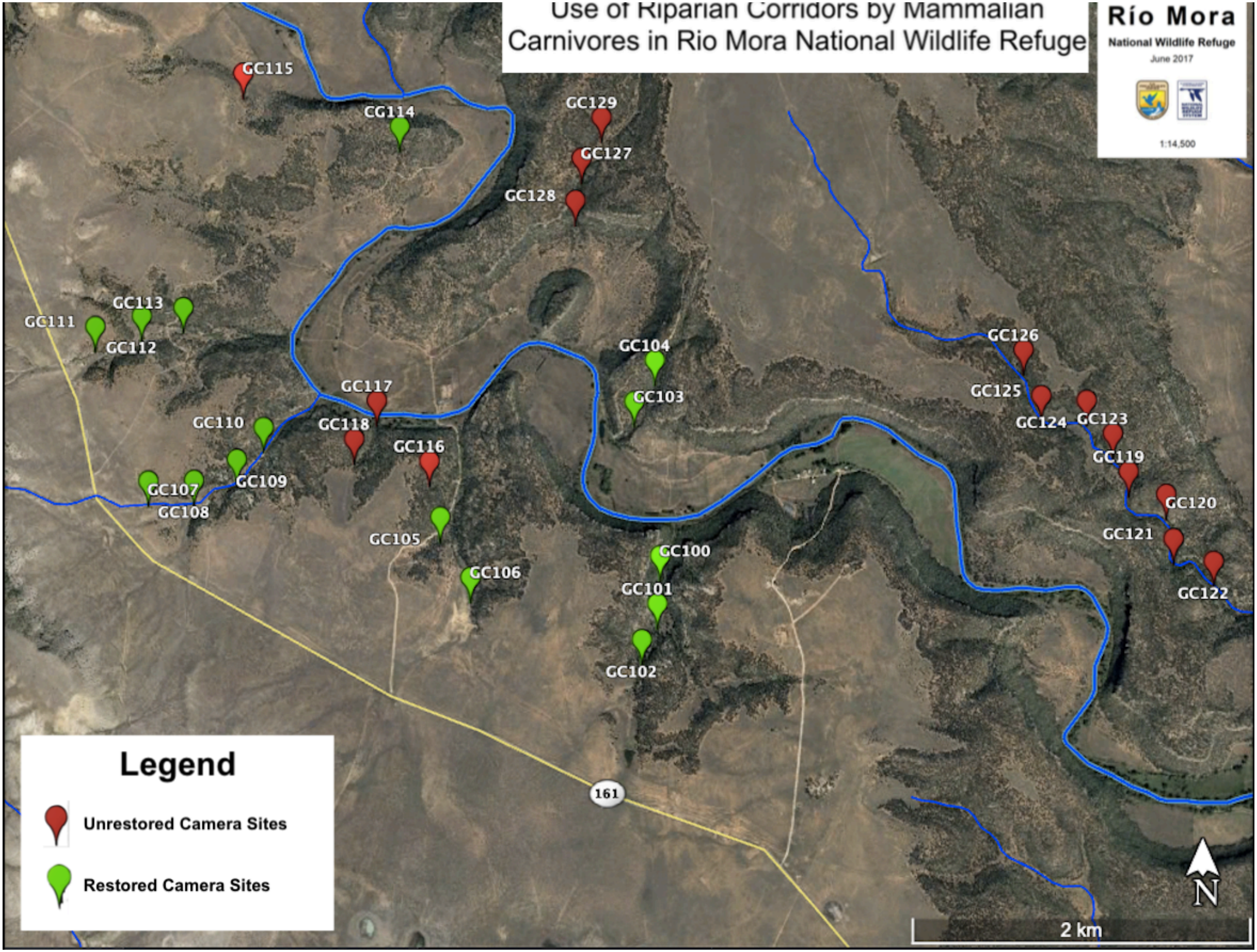


Figure 1: Map of camera site locations in Rio Mora National Wildlife Refuge. Locations in green denote camera sites in restored areas while locations in red denote camera sites in unrestored areas.

Vegetation Surveys

Vegetation surveys were done in-corridor from the center of the plot as well as in the riparian zone comprising 20m x 10m sections parallel to the corridor on both the left and right banks. I measured in-corridor canopy density using a spherical mirror densiometer and also compiled a list of woody species encountered in each plot.

In-Corridor Vegetation Survey

In-corridor surveys were done standing at the center of each plot. I classified the percent cover for each vegetation type (e.g. bare ground, forbs, grasses, shrubs) on a scale of 0 – 4 and determined vegetation densities at heights of <0.5m, 0.5m – 5m, and >5m using the same 0 – 4 scale (0 = 0%, 1 = ≤ 25% , 2 = 25–50%, 3 = 50–75%, 4= ≥75%).

Riparian Zone Vegetation Survey

Riparian zone vegetation surveys were done standing 5m away from the corridor banks on both sides of the corridor. I classified percent cover for bare ground, forbs, grasses, and shrubs using the same scale as the in-corridor vegetation surveys and determined vegetation densities at ≤0.5m, 0.5m – 5m, and >5m using the same scale as the in-corridor vegetation surveys. In cases where the riparian zone was inaccessible, data was later collected remotely using visual estimates of the same scale as before with Google Earth Pro.

Camera Trap Data

RMNWR deployed 30 Bushnell CAM HD Essential (Model: 119736C) camera traps (Fig. 1) in May 2016 to study wildlife unobtrusively. The cameras were set to take a photograph at 10-second intervals when detecting movement within a range of 36ft-100ft from the camera and were deployed for a total of 3 years.

Data Analysis

Corridor Morphology and Vegetation Surveys

Multivariate ordination analysis geometrically arranges sites so that the Euclidean distances between them in graphical ordination space accurately represents their distances in multivariate space. Thus, ordination is helpful in visualizing complex data using fewer dimensions and identifying patterns that can be further explored (Oksanen, 2011). All data analysis was done in R v3.6.2 (R Core Team, 2019). To ascertain how environmental characteristics differed between restored and unrestored canyons, I used a multivariate ordination approach. To do so, I calculated an environmental dissimilarity matrix using Gower's distance with the help of the StatMatch package (D'Orazio, 2011). I then conducted a nonmetric multidimensional scaling analysis using the metaMDS function in the vegan package in R (Oksanen et al., 2019). This resulted in two environmental axes to which I fit the environmental variables that described variation among sites (p-value < 0.01). Then, I used permutational multivariate analysis (Anderson, 2014) to assess the degree to which environmental characteristics differed by corridor and restoration status. To compare animal occurrences, I chose the subset of canyons that differed the most in environmental characteristics according to their distances in ordination space

Camera Trap Data

I used the package Machine Learning for Wildlife Image Classification 2 (MLWIC2) (Tabak et al., 2020) in R v3.6.2 (R Core Team, 2019) to parse through the more than 1.8 million photographs collected since 2016 in order to eliminate images with no visible wildlife. Machine learning algorithms are structures of layered neural networks that use artificial intelligence trained to recognize images much faster than the average person. These trained neural networks interpret raw data in the form of pixels through multiple layers of recognition that increase in complexity as the layers progress (Norouzzadeh et al., 2018). I used the “empty animal” model in the MLWIC2 package to classify all animal occurrences, including potential prey species, for the cameras located in the two canyons that differed the most in their environmental characteristics: Falcon and Petroglyph. The “empty animal” model recognizes whether an animal is present in the image. After reducing the number of photographs from Falcon and Petroglyph canyons that did not contain any animals using the empty animal algorithm, I manually classified the remaining images the algorithm marked as having an animal present in the image and recorded the number of occurrences at each site for all species encountered as species abundance. All instances of humans and domesticated animals were excluded from the analysis. I also noted presence and absence for all relevant species encountered at camera site. Since I only had data from three camera traps within each canyon, I conducted a bootstrap analysis (Chernick et al., 2011) of the species abundance and presence/absence data, resampling both data sets 10,000 times to generate confidence intervals for the difference in mean abundance between the two sites. I also used a permutation test (Hallin & Ley, 2014) to test for significant differences in mean abundance and occupancy.

Linking Environmental Characteristics and Camera Trap Data

To assess whether differences in species composition in Falcon and Petroglyph canyons was correlated to differences in their environmental characteristics, I first created a Bray-Curtis species dissimilarity matrix using the ade4 package (Dray & Durfour, 2007) for both species abundance and species presence/absence. I then performed a Mantel test (Giraldo et al., 2018) to determine whether environmental distance between sites correlated with difference in species composition. I also used permutational analysis of variance (Anderson et al., 2014) using the adonis function in the vegan package (Oksanen et al., 2019) to assess whether environmental ordination scores correlated with species composition within the two canyons.

Results

Corridor Morphology and Vegetation

NMDS ordination of all environmental variables resulted in a two-dimensional ordination with a stress level of 0.17. The first axis describes riparian zone characteristics, corridor height, and corridor accessibility, while the second axis described in-corridor characteristics, water presence, corridor slope, and the presence of some woody plant species (Figure 3). Habitat structure differed more by canyon than by restoration status. Approximately 46% of the variation between sites was explained by corridor-level differences ($p = 0.02$). Conversely, restoration status accounted for a significant ($p = 0.05$) but much smaller proportion of variance at 6%. According to the distance in ordination space, cameras GC100, GC101, and GC102 in Falcon canyon as sites 1, 2, and 3 were most dissimilar from GC108, GC109, and GC110 located in Petroglyph canyon denoted as sites 9, 10, and 11 (Figure 3).

The transition between upland prairie and rocky, incised terrain is much more pronounced in Falcon canyon while Petroglyph canyon is much more gradual in its transition from prairie soil to exposed bedrock. Environmental differences between Falcon and Petroglyph canyons are evident from the photographs from each camera trap (Figure 4 & Figure 5). GC102 faces upstream and overlooks the entrance to Falcon canyon from the upland shortgrass prairie. This area contains a small ephemeral stream and is populated by a vegetation community of grasses and forbs, willow stands, piñon pine, and juniper trees (Figure 4A). As we move further downstream into the canyon, GC101 is located between two steep banks of exposed rock and overlooks a small field with grasses, piñon pine, juniper trees, and willow stands as the main vegetation in this area (Figure 4B). GC100 is located further downstream and overlooks a rocky area with steep banks on either side, exposed boulders, and less undergrowth vegetation comprised mainly of oak, piñon pine, and juniper trees (Figure 4C). In comparison to Falcon canyon, the upstream terrain of Petroglyph canyon is much more open. GC108 is located in the ecotone between the upland shortgrass prairie and piñon-juniper woodland of Petroglyph canyon and overlooks the convergence of two arroyos (Figure 5A). GC109 is located in much flatter terrain further downstream with sections of undefined banks and juniper trees, grasses, and willow stands making up the vegetation community (Figure 5B). Following the corridor downstream, GC110 is located after a steep drop in elevation, forming pronounced corridor banks and exposing the canyon bedrock. The area overlooked by the camera has a pool with sparse grass and willow stands which become much more dense downstream (Figure 5C).

Camera Trap Data

A little over half of the 15 species observed in Falcon and Petroglyph canyons are medium-large predatory mammals. The remaining 7 are almost all herbivorous mammals with the exception of wild turkeys (*Meleagris gallopavo*) (Table 1). Almost all species were found in both canyons except pronghorn (*Antilocapra americana*) and black-tailed jackrabbit (*Lepus californius*) that were observed only in Petroglyph canyon, and spotted skunks that were only observed in Falcon canyon (Table 1). The number of occurrences per species and species richness varied between canyons as well with a greater proportion of sightings occurring in Falcon canyon and greater species richness in Petroglyph canyon (Figure 6 & 7). Although the average number of animal sightings did not significantly differ between the two canyons ($p = 0.8$), Falcon canyon witnessed on average 269 more sightings than Petroglyph canyon. On the other hand, average species richness was higher in Petroglyph canyon than in Falcon canyon with an average of 3 more species, but this difference was also not statistically significant ($p = 0.2$).

Despite minimal differences in overall diversity between the two canyons, the bootstrap analysis for species occurrence revealed significant differences ($p < 0.05$) in species occurrence between the two canyons for 6 out of the 15 species. Coyotes, elk, striped skunk, black-tailed jackrabbit and pronghorn were more prevalent ($p < 0.001$) in Petroglyph canyon, while spotted skunk was more prevalent ($p < 0.001$) in Falcon canyon. For most species, abundance did not differ between Falcon and Petroglyph canyons. Of the 14 species observed in Falcon and Petroglyph canyons, only three showed significant differences ($p < 0.05$) in abundance. Spotted skunks were observed exclusively in Falcon canyon ($p < 0.001$), while black-tailed jackrabbits and pronghorn were observed 16 ($p < 0.001$) and 0.33 ($p < 0.001$) more times in Petroglyph canyon respectively.

Linking Environmental Characteristics and Camera Trap Data

Environmental factors marginally explained the differences in number and abundance of species observed between Falcon and Petroglyph canyons. The Mantel test correlating environmental characteristics to species abundance revealed that they are marginally correlated (R^2=0.738, p= 0.07). The same test correlating environmental characteristics to species presence/absence found that they are marginally correlated as well (R^2=0.497, p=0.07). Despite these significant positive correlations, permutational multivariate analysis of variance (PERMANOVA) tests showed that mammalian community structure in Falcon and Petroglyph canyons was not significantly correlated to either of the environmental axes (NMDS1 $p = 0.3$, NMDS2 $p = 0.5$). The same can be said about the PERMANOVA test for the species presence/absence matrix and environmental scores for both environmental axes (NMDS1 $p = 0.3$, NMDS2 $p = 0.5$).

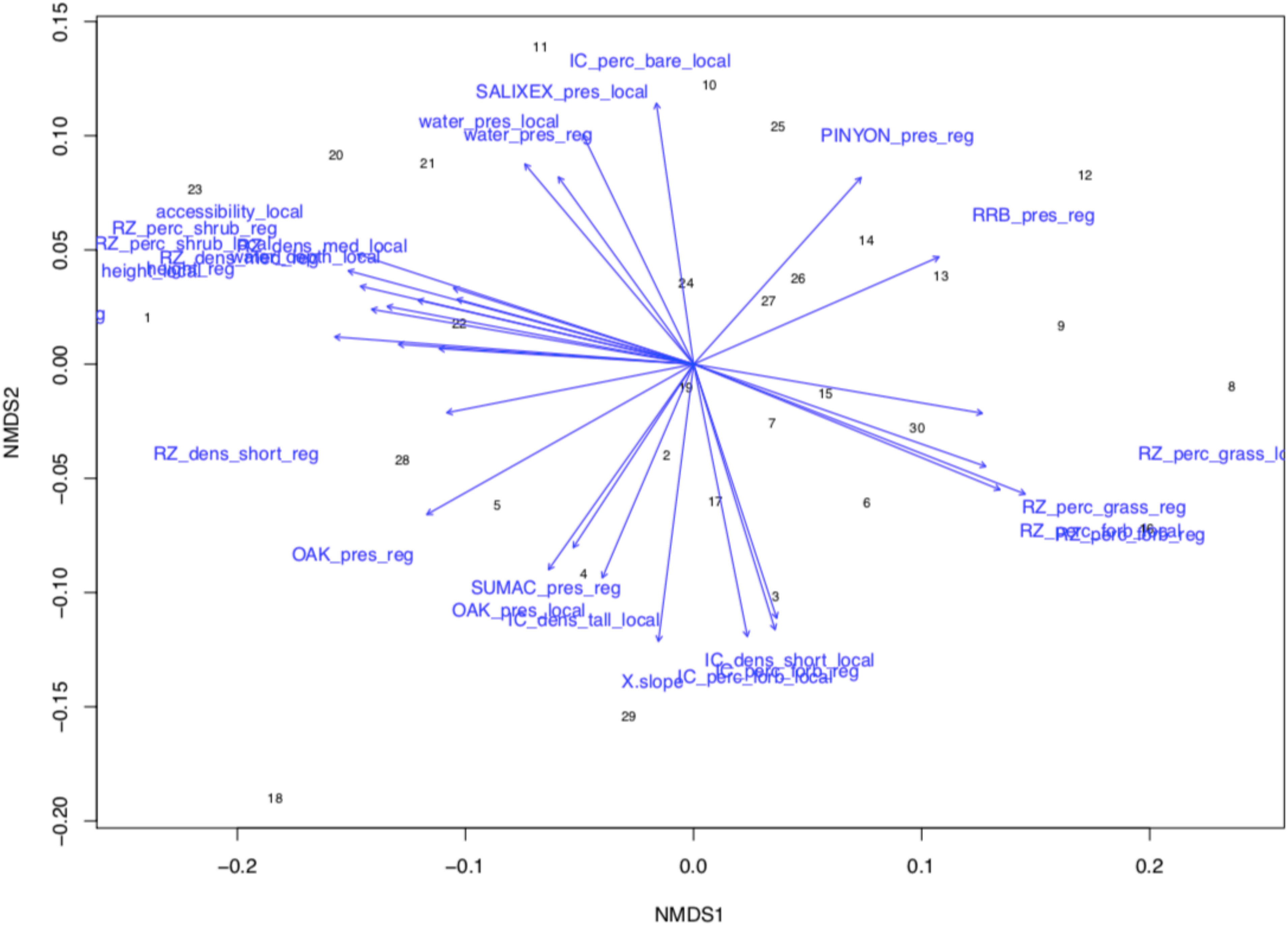
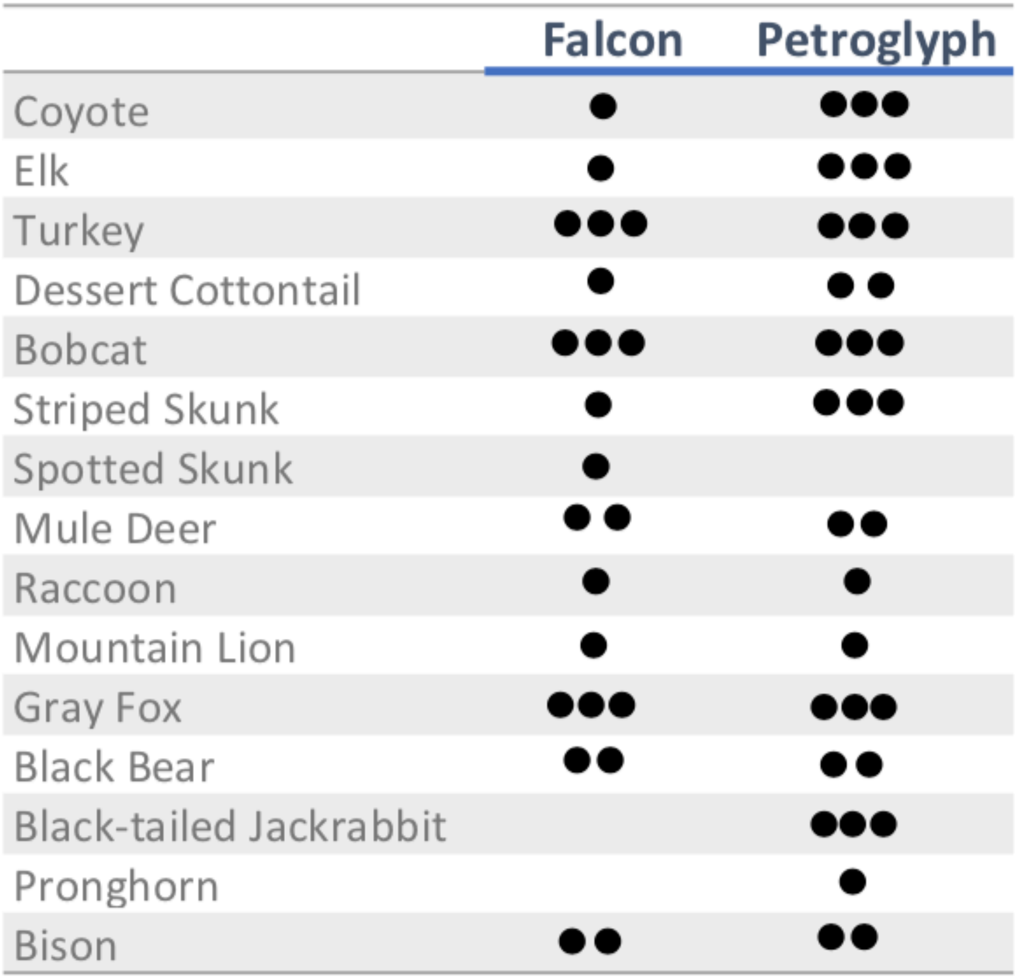


Figure 3: Position of sites in ordination space according to environmental dissimilarity distances. Sites 1 – 3 correspond to GC100, GC101, and GC102. Sites 9 – 11 correspond to GC108, GC109, and GC110. Blue arrows denote significant (p<0.01) environmental variables.

Figure 4: Camera site locations at Falcon Canyon. A: Location of GC102 (site 3). B: Location of GC101 (site 2). C: Location of GC100 (site 1).

Figure 5: Camera site locations at Petroglyph Canyon. A: Location of GC108 (site 9). B: Location of GC109 (site 10). C: Location of GC110 (site 11).

Table 1: Species occurrences at Falcon and Petroglyph canyons. Dots represent a species' detection at a camera site at Falcon or Petroglyph canyons.



	Falcon	Petroglyph
Coyote	●	●●●
Elk	●	●●●
Turkey	●●●	●●●
Dessert Cottontail	●	●●
Bobcat	●●●	●●●
Striped Skunk	●	●●●
Spotted Skunk	●	
Mule Deer	●●	●●
Raccoon	●	●
Mountain Lion	●	●
Gray Fox	●●●	●●●
Black Bear	●●	●●
Black-tailed Jackrabbit		●●●
Pronghorn		●
Bison	●●	●●

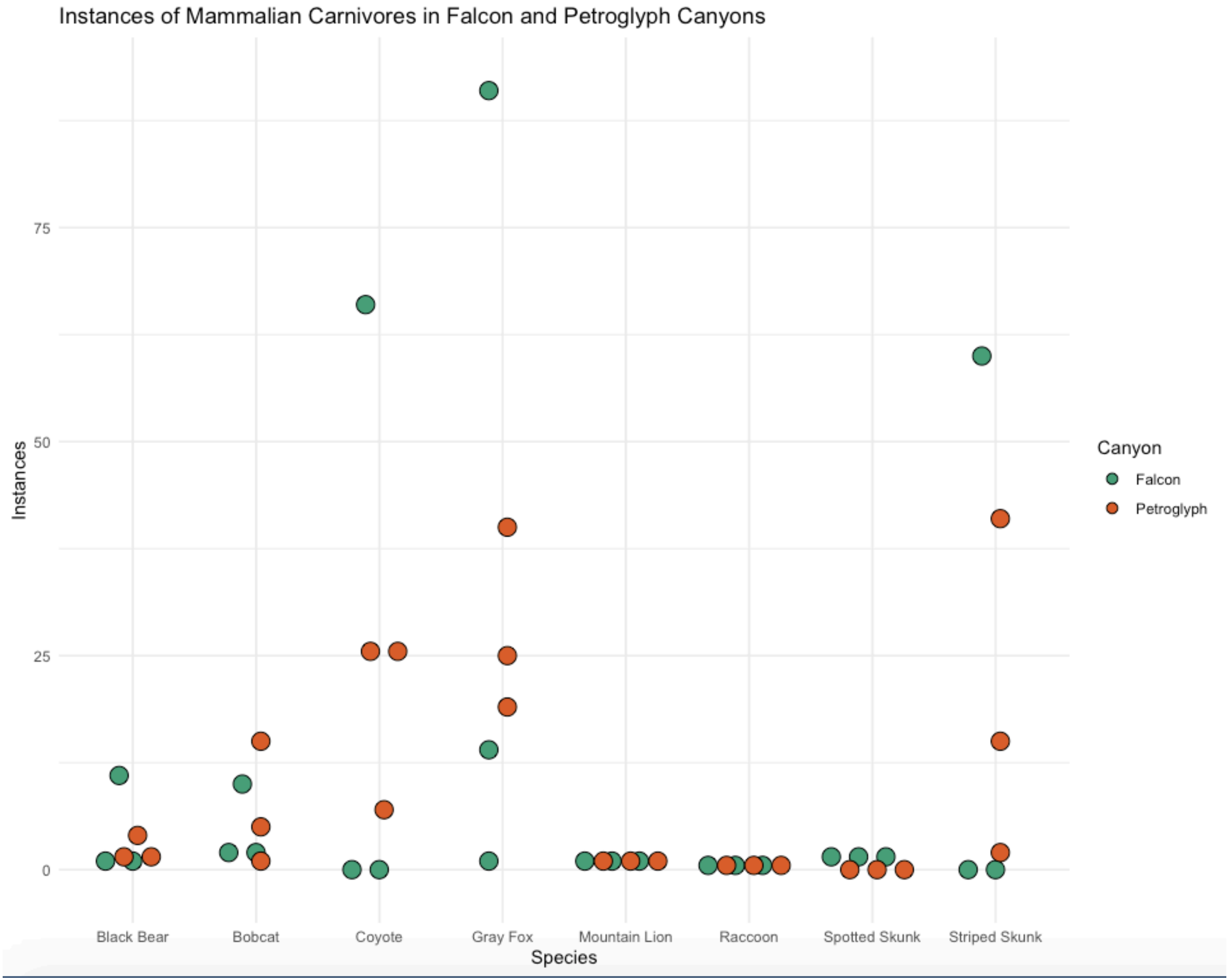


Figure 6: Number of instances of mammalian carnivores captured in Falcon and Petroglyph canyons

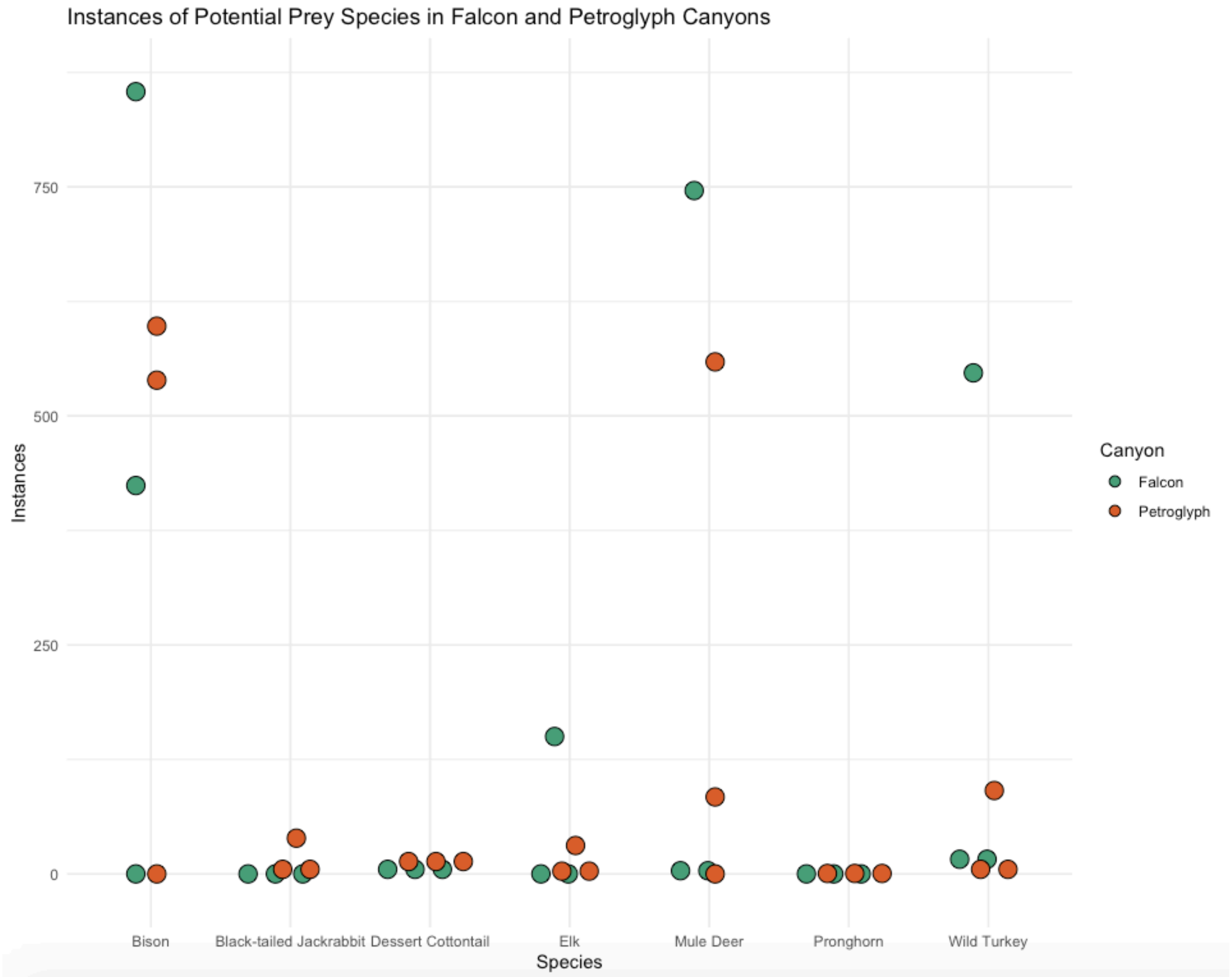


Figure 7: Number of instances of potential prey species captured in Falcon and Petroglyph canyons.

Discussion

My prediction that restored corridors would show a greater degree of usage by mammalian carnivore species and their prey was not supported because habitat differences were stronger among sites in different canyons than between restored and unrestored sites. These canyon-level differences in habitat structure only modestly correlated to differences in mammalian occupancy and abundance since most species were observed at similar rates in both canyons. Fewer species differed in their average prevalence between canyons, and even fewer differed in average number of sightings. Although carnivorous species were observed in both canyons (e.g. black bear, bobcat, coyote, gray fox, mountain lion, raccoon, and stripped skunk), a few potential prey species were more prevalent in Petroglyph rather than Flacon canyon. More prey species were observed in Petroglyph canyon because two of the species (e.g. black-tailed jackrabbit and pronghorn) are associated with habitat features only found in Petroglyph. Because of these results, it was unsurprising that species richness and total abundance of mammals showed no strong differences across canyons. In summary, the effects of canyon habitat structure tended to relate only modestly to mammalian community structure in the two canyons analyzed in this study.

When explaining the differences in habitat structure between sites, canyon-level differences such as canyon height, accessibility, slope, ground cover type, and the presence of certain woody plant species, rather than restoration status accounted for a greater proportion of variance in habitat between sites. The low percentage of variation between sites explained by restoration status could be attributed to the amount of time elapsed since arroyo restoration structures were installed. Indeed, Wissmar and Beschta, (1998) and Montgomery and Bolton (2003) caution that restoration activities which modify hydrology may not immediately result in habitat changes because the recovery of ecosystem processes can take up to several decades to return. RMNWR began installing one-rock dams in 2012, so the time horizon for recovery has been limited. Since there is a strong potential for feedback between vegetation, corridor form, and channel processes (Montgomery & Bolton, 2003), the deployment of one-rock dams and other structures to reduce the speed of water in these corridors may not have had enough time to change the environmental characteristics at these sites.

Although we did observe significant differences in habitat features in Petroglyph and Falcon canyons, these did not translate to strong differences in mammalian occupancy. One reason for this could be that animal abundance and corridor usage are more realted to features we did not measure in the corridor or in the surrounding landscape (Zimbres et al., 2017). For example, in the Amazonian rainforest, Lees and Peres (2008) showed that the composition of the vegetation community was important for determining mammalian community structure. However, my measure of vegetation community was limited to presence/absence of woody species which may have been to coarse to show strong differences in the vegetation community. In addition, corridor use by wildlife may be more strongly controlled by habitat features outside of the corridor itself. The spatial configuration of surrounding landscapes (Prist et al., 2012), the harshness of the landscape outside the corridor (Umetsu et al., 2008), and the quality of habitat patches that the corridor connects (Lindenmayer, 1994) have all been shown to influence corridor use, but were not included in this study.

Despite the lack of strong differences in mammal community structure between Falcon and Petroglyph canyons, environmental structure and species abundance and occurrence were marginally correlated. A few species differed in their rate of occurrence between the two canyons, and these differences can be explained by contrasting habitat features in the canyons.

Although not significant, the differences in total mammal abundance between Falcon and Petroglyph canyons could be attributed to the greater availability of cover provided in Falcon canyon. Most species observed in the canyons were those of potential prey, which require adequate cover to protect against predation (Dickie et al., 2020). For example, spotted skunks were only observed in Falcon canyon which had a denser, more complex understory that the spotted skunk prefers to reduce predation risk (Lesmeister et al., 2009). Petroglyph canyon supported a more open habitat that lacked such cover. On the other hand, black-tailed jackrabbit and pronghorn were only found in Petroglyph canyon. Black-tailed jackrabbits have been shown to prefer habitat with a mixture of open grassland and shrub cover (Marín et al., 2003), both of which are prevalent in Petroglyph canyon. Pronghorn are associated with upland prairie habitat (Poor et al., 2012) of which a large portion can be found in Petroglyph canyon. Because of the higher presence of prey, like the black-tailed jackrabbit in Petroglyph canyon, coyotes were also more likely to be observed there (Bender et al., 2017). Petroglyph canyon also provides habitat with increased visibility, a characteristic that Elk favor in order to reduce predation risk (Pitman et al., 2014) and they were also more likely to be observed in Petroglyph canyon. Striped skunks are more generalist in their habitat selection and show little preference for one habitat type over another (Neiswenter & Dowler, 2007) so they were observed much more evenly between both canyons.

Further work is needed to fully describe the effects of environmental structure on animal visitation rates in the canyons of RMNWR. Due to time constraints, abundance and occurrence events were only analyzed for two out of the ten canyons containing camera traps at RMNWR. To gather a more complete picture of how animal communities use the corridors at RMNWR, including all 30 camera sites in the analysis is the next step and will better show how habitat structure and animal abundance and occurrence correlate for the whole refuge. In addition, understanding how habitat characteristics like vegetation composition vary seasonally may better account for variation in wildlife visitation rates and animal occupancy (Zimbres et al., 2017). Finally, describing diurnal and seasonal animal visitation can more finely resolve how species use their habitat and can result in a better understanding of how competitors may partition their use of habitat (Hale et al., 2020).

Restoration in canyons at RMNWR has not yet had enough time to effect changes in habitat for the medium-large mammals that use the corridors at the refuge. While canyons differed in key habitat features such as ground cover type and height, these differences did not ultimately result in substantial differences in mammalian visitation. These results can have broad impacts for habitat and species management at RMNWR and other semi-arid areas by providing managers with specific canyon characteristics to improve for a targeted species of interest. In fact, Hale et al. (2020) suggest that restoration efforts like those undertaken at the refuge should focus more on habitat requirements based on species behavior of specific species rather than passive restoration through changes in vegetation community and conclude that measuring key aspects of fitness like breeding and survival should be monitored. Knowing which habitat characteristics are preferentially selected by the animal community at RMNWR and monitoring key aspects of fitness can help inform decisions on which areas need more focused restoration efforts if the goal is to have persistent populations of animals using the corridors at RMNWR.

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CHAPTER 4.

Reintroduction and Human-Carnivore Conflict Mitigation of The Grey Wolf (*Canis lupus*) in Historical Ranges in Western Colorado

Wolf reintroductions to historical ranges in western Colorado will be on the voting ballot (Initiative 107, Colorado Grey Wolf Reintroduction Initiative) this coming November 2020. If successful, the measure will require the Colorado Parks and Wildlife Commission to create a plan based on the best science available for wolf reintroduction and management by the end of 2023 (Colorado Secretary of State, 2020). Reintroducing wolves to parts of their historical range in Colorado as keystone apex predators will reinstate several ecological benefits that wolves provide. These benefits include those of top-down regulation of prey species, usually overabundant ungulates, through predation or behavioral changes that may cascade to affect lower trophic levels (Newsome et al., 2015; Ripple & Larsen, 2000). The most important result of restoring top-down control is an increase in biodiversity that results from reduced foraging pressure by herbivores, which in turn increases the resilience of the ecosystem to disturbance. Foraging from overabundant ungulate populations can restructure plant communities (Bradford & Hobbs, 2008; Pedersen & Wallis, 2004), reduce abundances of other wildlife such as birds (Berger et al., 2001), insects (Miyashita et al., 2004), and soil arthropods (Wardle et al., 2001). Overabundant ungulate populations can also influence biogeochemical cycles through foraging pressure by changing the distribution of nitrogen in an ecosystem (Harrison & Bardgett, 2004).

Despite these ecological benefits, opposition to wolf reintroduction from coalitions of ranchers, farmers, hunters, and outdoor recreationalists is quite strong. These groups not only worry that wolves might prey upon livestock and endangered or threatened species, but also that the budget required to manage wolves will take away funds from other important projects. In addition, wolves may compete with hunters for game species, compromise the safety of those who participate in outdoor activities, and be challenging to manage. Re-establishing viable populations of wolves in western Colorado can result in broader benefits to the ecosystem and economy if conflicts with humans are mitigated through stakeholder inclusion, coexistence strategies, fair compensation in the case for livestock loss, and outreach and education programs detailing the ecological and economic benefits of established wolf populations.

Gray wolves (*Canis lupus*) once occupied nearly all of North America, but like many other large carnivores, were persecuted and extirpated by European settlers who valued safety on their newly acquired land. Settlers also degraded wolf habitat by depleting and degrading resources that wolves use (U.S. Department of Justice, 2018). By the early 20th century, habitat degradation and extensive predator control programs supported by attractive bounties nearly extirpated all wolves from the lower 48 states (U.S. Department of the Interior, 2016). In Colorado, wolves were eradicated by 1940 with no evidence of a sustainable local population in the state since that time (Colorado Parks and Wildlife, 2019).

Following almost complete eradication, recognition of the plight of gray wolves caused public sentiment towards wolves to shift, and the gray wolf was federally classified as a protected species in the 1960s. These protections were further strengthened by the passage of the Endangered Species Act (ESA) in 1973 and by listing gray wolves as endangered in 1974. Following a decade-long effort to implement an ESA-mandated recovery plan, wolves captured in Alberta, Canada were reintroduced to central Idaho and Yellowstone National Park (YNP), Wyoming in the 1990s. The recovery plan also supported natural migration of wolves into northwestern Montana from Canada (Wilson, 2006). Today, gray wolves can be found in the western Great Lakes, northern Rocky Mountains, throughout much of Alaska, and the Southwest U.S. (Houston et al., 2010). In 2002, the U.S. Fish and Wildlife Service (USFWS) proposed delisting wolves as federally endangered, and in 2009, USFWS removed the northern Rocky Mountain population of gray wolves from protections under the ESA, leaving the management of wolf populations under state control (Houston et al., 2010; Wilson, 2006). Although migration into Colorado from wolf populations in surrounding states has been recorded, illegal or accidental killings have prevented natural dispersal into Colorado, necessitating the call for a protected reintroduction (Carroll et al., 2003; Mech, 2017).

Stakeholders in favor of wolf reintroduction to western Colorado include local, state, and national conservation groups such as the Rocky Mountain Wolf Action Fund, the Colorado Wolf and Wildlife Center, the International Wolf Center, and the Sierra Club. These groups represent people that include outdoor recreationalists, hunters, private landowners, and citizens of Colorado who understand the value that wolves, as apex predators, bring to a system where it has been missing for an extended period of time. Aside from being represented by organizations, individual outdoor recreationalists, hunters, private landowners, and citizens of Colorado are also stakeholders in favor of this decision.

A number of outdoor recreationalists favor the reintroduction of wolves to western Colorado because they understand and value the benefits of a healthy and diverse ecosystem where they spend leisure time. Some hunters, probably more than any other stakeholder, understand and value the importance of predators in maintaining the health and viability of game populations (Granoth-Wilding et al., 2017). A cornerstone of ecology is the positive relationship between an ecosystem's biodiversity and its ability to maintain important ecosystem functions like nutrient cycling and a disease regulation (Balvanera et al., 2006; Chapin et al., 1997; Hooper et al., 2005; Wild et al., 2011). By keeping prey abundance in check or altering prey behavior, apex predators exert top-down control that enhances the coexistence of multiple species so that one does not outcompete the others (Allesina & Tang, 2012; Miller et al. 2001). Hunters also understand that by targeting weak, old, or sick individuals, wolves may reduce the prevalence and transmission rates of diseases, such as Chronic Wasting Disease (CWD) within their preferred game species populations (Wild et al., 2011).

Evidence of beneficial ecological effects of apex predator reintroductions are ubiquitous throughout reintroduction sites, but none is more famous than the reintroduction of wolves and other predators to Yellowstone National Park. In the absence of wolves, Rocky Mountain elk (*Cervus elaphus*) dramatically increased in numbers and altered the vegetation community by overbrowsing and displacing other keystone species such as beavers (*Castor canadensis*) (Beschta & Ripple, 2019). After wolves were reintroduced to Yellowstone, elk modified their foraging behavior leading to a cascade of effects that included renewed vegetation growth initiated by re-established beaver populations (Marshall et al., 2013). Because they rely on riparian vegetation for cover and food, fish and songbird populations also increased (Berger et al., 2008; Ripple & Beschta, 2012). Wolf reintroduction also reinstated top-down control of mesopredators. In the absence of top-down control from an apex predator, generalist mesopredators such as coyotes (*Canis latrans*) explode in numbers, leading to the overconsumption of small mammal species and loss of other mesopredators such as foxes (*Vulpes* spp.). Conversely, when wolves are reintroduced, mesopredator numbers are held in check, reducing competition and predation lower in the food web (Barnowe-Meyer et al., 2010; Berger et al., 2001; Newsome & Ripple, 2015; Ripple et al., 2011). Wolves also provide carrion from left-over kills that are an important food source for mesopredator communities (Wilmers et al., 2003). This evidence suggests that wolf reintroductions to Colorado will have similar cascading effects that will benefit various environments across western Colorado.

Private landowners and other citizens located in the proposed reintroduction hope that wolf reintroductions will establish the reintroduction zones as hubs for increased ecotourism as it has in Yellowstone (Staff, 2019; Wilson, 2020). Wolves have become one of the primary reasons for visiting YNP. This popularity is due in part to wolves being extremely visible compared to other predators like elusive mountain lions and hibernating bears. Wolves can be seen during most of the year and are much more active as social groups in open landscapes, allowing them to be more easily spotted by wildlife enthusiasts (Staff, 2019). Wolf popularity in YNP has fostered communities of wildlife viewing companies, educational associations, and groups of wolf watchers that contribute approximately $35 million annually to local economies (Duffield et al., 2008; Smith et al., 2016). Communities in the proposed reintroduction sites in western Colorado can use YNP as a model for establishing a wolf ecotourism economy that can offset the costs of maintaining wolf populations in the area.

Although some stakeholders perceive wolves as beneficial species that maintain ecosystem functions and provide economic opportunities, other stakeholders oppose wolves because of their roles as predators in ecosystems. These include coalitions of ranchers, farmers, private landowners, hunters, and outdoor recreationalist organizations across the state, including the Stop the Wolf Coalition, the Colorado Farm Bureau, the Rocky Mountain Elk Foundation, Coloradans Defending Our Wildlife, and Coloradans Protecting Wildlife. These stakeholder groups represent individuals who believe their economic interests will be disproportionately affected by the ecological changes that wolf reintroduction will set in motion.

One such group that fervently opposes wolf reintroduction is ranchers and farmers. Ranchers and farmers value their livelihood, and wolf reintroduction compromises their ability to economically sustain this livelihood. They fiercely oppose the reintroduction of wolves because wolves may kill livestock, ultimately depressing profit margins. Developing and implementing strategies to mitigate and prevent livestock losses is essential to changing these stakeholders' attitudes towards wolf reintroduction. There are no livestock protection tools that serve as "silver bullets," but a combination of site- and operation-specific tools may help prevent direct losses of livestock and minimize the indirect impacts of wolf presence (Macon et al., 2018; Stone et al., 2017). These tools must be effective, economically beneficial, and socially and legally acceptable (Macon et al., 2018; Miller et al., 2016; Young et al., 2011). Such tools include the lethal control of "nuisance" individuals under supervision of the state's wolf managers, the use of livestock guardian animals, the implementation of protective fencing, removal of attractants such as dead animals, the use of human presence such as herders, fright tactics and devices, and husbandry and management changes to reduce encounters with wolves (Macon et al., 2018; Miller et al., 2016). The costs of these tools and their implementation can be offset through what would essentially be a state "wolf tax" on the newly created wolf ecotourism sector and their effectiveness can be determined alongside state wolf managers when conducting wolf surveys. In the event of livestock loss from wolf predation, the measure to reintroduce wolves to western Colorado includes state funds to pay fair compensation to owners of livestock for any losses caused by grey wolves.

Hunters as well as some state wildlife managers believe that adding a predator that competes with hunters for game species will reduce the number and quality of game in reintroduction areas. The fear is that this would reduce the amount of big game licenses from which the state obtains a majority of its funds to manage and conserve other species of concern. On the other hand, big game populations could thrive under the effects of ecological restoration of top-down control and selective wolf predation. Some wildlife managers are also against the reintroduction of wolves because it would financially and logistically strain the limited management resources that already exist to manage threatened wildlife populations. Informing declining populations of hunters that hunting alone is insufficient to maintain game species populations from growing uncontrolled and that wolves prevent the spread of diseases by targeting sick individuals may change opinions on the reintroduction of wolves. To assuage fears that wolves may decrease game populations, state wildlife managers can partner with hunters to monitor population trends of big game populations. State wolf managers could also partner with private stakeholders interested in being involved with the newly created ecotourism sector by providing grants funded from the "wolf tax" or other state allocated funds for new private or public wildlife technician or wildlife biologist jobs.

These positions would gather data on the reestablishing wolf packs directly through wolf surveys, or indirectly through the management of citizen science-gathered data. Gathering population data on the reestablished wolf packs is essential to informing management decisions and changing negative public perceptions (Glikman et al., 2012). Monitoring studies on newly reestablishing wolf packs in Finland have shown that citizen science data collected by local hunters and outdoor recreationalists was an effective and low-cost tool for non-invasive GPS telemetry and genetic monitoring of wolf packs (Granroth-Wilding et al., 2017; Kojola et al., 2018)

Members of the general public who oppose wolf reintroduction include some outdoor recreationalists, private landowners, and private citizens of Colorado. Their opposition stems mainly from a perceived risk of encountering a potentially dangerous carnivore. In order to change public opinion on wolf reintroduction, implementing educating programs about wilderness safety and wolf ecology may prove successful. Similar programs and studies in Illinois (Landon et al., 2019) and central Italy (Glikman et al., 2012) concluded that increasing the public's knowledge on the species with factual information helped assuage perceived fears of public safety. Informational campaigns (Landon et al., 2019), especially if based on data gathered by citizen scientists like those implemented in Finland (Granroth-Wilding et al., 2017; Kojola et al., 2018), may similarly change the public's perspective from one of fear to one of local land stewardship. Including members of stakeholder groups typically opposed to reintroduction in the wolf management process can expose them to favorable interactions with wolves like those of the volunteers in Granroth-Wilding et al. (2017) and Kojola et al. (2018). These favorable interactions can change their overall attitudes towards this unfairly persecuted predator (Meadow et al., 2005).

The reintroduction of grey wolves to areas of western Colorado is possible if stakeholders understand and value the overall ecological and economic benefits that reintroduction would entail. Changing the public's perception about living alongside wolves can be accomplished by including stakeholders in the management process. Working closely with ranchers and farmers located in the reintroduction areas to prevent and mitigate livestock loss is an essential step to changing their attitudes about wolves. Involving hunters, outdoor recreationalists, and the general public in the study of the newly established wolf populations will foster a sense of stewardship for the species and will lead to the creation of jobs and opportunities funded by the newly created ecotourism sector. The ecotourism sector created because of the popularity of wolves as seen in YNP could offset many of the costs associated with the management of wolf populations and fund various projects involving other species of concern. Finally, widespread educational campaigns based on data collected by stakeholders and hosted by wolf managers can diffuse factual information on the ecology, behavior, and benefits of having wolves in their backyard and support carnivore reintroduction efforts.

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