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CAPSTONE PROJECT

by

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CHAPTER 1. LITERATURE REVIEW

Mitigating Human-Coyote Conflict Requires an Understanding of What Facilitates Coyote Use of Urban Spaces

Introduction

As the most prevalent large carnivore in urban areas of North America Coyotes (*Canis latrans)* are a source of many human-wildlife conflicts. Coyotes expanded their range from the western plains of the continent in the 1800s, into nearly all of North and Central America by the 2000s (Gompper, 2002; Hody & Kays, 2018). Ecological release of coyotes was likely facilitated by the elimination of wolves and other large predators, coyote hybridization with other wild and domestic canid species, and creation of more suitable habitat through increased transformation of land for farming and ranching (Hody & Kays, 2018). Coyotes have also moved progressively into cities, leading to more contact with humans and interactions that have become increasingly antagonistic (Baker & Timm, 2017; Bateman & Fleming, 2012; Howell, 1982; Mowry et al., 2021; Poessel et al., 2013).

As humans continue to expand into previously undeveloped areas and coyotes venture farther into cities, it is reasonable to expect human-coyote interactions to continue. This paper will explore the factors that contribute to coyote use of urban habitat, including behavioral adaptations of coyotes, their use of facets of the built environment, dietary differences between urban and rural populations, and how these factors relate to human-coyote conflict. Finally, it will argue that the best way to mitigate conflict is through changing aspects of human behavior and the built environment and will suggest specific actions based on what is known about coyote use of urban areas at this time.

Behavioral Adaptations of Coyotes in Urban Environments

Behavioral plasticity is the ability of an individual to make short-term adjustments to their behavior in response to changes in their environment (Snell-Rood, 2013). Such behavioral adaptability is essential to the success of urban animals and is observed in many species (Fischer et al., 2012; McKinney, 2002; Newsome et al., 2015; Santini et al., 2019). Like other urban species, coyotes have a unique level of behavioral plasticity that enables them to take advantage of cities (Baker & Timm, 2017; Gese et al., 2004). Examples of behavioral plasticity seen in urban coyotes include temporal shifts and an increase in bold behavior (Breck et al., 2019; Franckowiak et al., 2019; Grinder & Krausman, 2017; Sol et al., 2013). These changes in behavior can result in coyotes encountering humans more frequently, which can lead to more conflict (Breck et al., 2019; Mcclennen et al., 2001).

Coyotes are able to shift their daily activity patterns in response to changes in their environment, such as human presence, as seen in the differences in temporal patterns are observed between rural and urban populations. Coyotes in rural areas are significantly more active during the day than coyotes in urban areas (Mcclennen et al., 2001). Coyotes in cities are more nocturnal, and less active around dawn and dusk, with activity peaking around midnight as coyotes wait out the higher level of human activity in the evening (Gese et al., 2012; Grinder & Krausman, 2017; Grubbs & Krausman, 2019). Increased activity at night is likely a technique to avoid human presence, and therefore contributes to the success of coyotes in human-dominated areas (Gese et al., 2012; Tigas et al., 2002).

While coyotes are more active at night in urban areas, they are also observed in broad daylight (Gehrt, 2007). Daytime presence is likely a result of an increase in bold and exploratory behavior among individual coyotes in these areas (Breck et al., 2019; Gehrt, 2007; Way et al., 2004). Bold behavior is a desensitization to the presence of a potential threat and an increase in risk-taking (Breck et al., 2019; Schell et al., 2018). For example, bold coyotes are less likely to flee as humans approach. Exploratory behavior is the response of an individual to a novel object (Breck et al., 2019; Ritzel & Gallo, 2020). Urban coyotes that are more exploratory are likely to investigate new developments in their environment more readily than their rural counterparts. In urban areas this means that individuals are not scared off by the presence of human disturbance and can therefore take advantage of various anthropogenic resources that would otherwise be off-limits (Breck et al., 2019; Schell et al., 2018).

The importance of the behavioral plasticity of coyotes in their use of the urban environment becomes clear when they are compared with a similarly sized carnivore that is often found on the edges of urban development—bobcats (*Lynx rufus)*. Both bobcats and coyotes are observed to shift to more nocturnal activity in urban areas (Crooks, 2002). However, coyotes are more likely to take advantage of elements within the built environment than bobcats, which have a greater aversion to human presence (Tigas et al., 2002). Coyotes are also found more commonly in higher housing density, and across all urban areas, than bobcats (Crooks, 2002; Parsons et al., 2019). The higher level of tolerance for human activity seen in coyotes over other carnivores contributes to their successful use of cities (Murray & St. Clair, 2017; Riley et al., 2003). Coyotes are also found in much smaller fragments of natural habitat than bobcats, facilitating their use of the spaces that remain after the intense fragmentation of human development (Crooks, 2002). Greater behavioral adaptability and use of highly developed landscapes compared to similarly sized mammals is a large part of why coyotes prevail in urban areas when other species do not.

Conflict between humans and coyotes can be driven by each of the different behavioral adaptations of coyotes. The shift of urban coyotes to limited times of activity could lead to an increase in the level of activity when they are active overnight, making it more likely that they will come into contact with humans (Mcclennen et al., 2001). Additionally, coyote behavioral adjustments are at least partially a result of human actions. In urban areas people are more tolerant, or even encouraging of coyotes, which decreases their fear response and leads to an increase in bold and exploratory behavior (Baker & Timm, 2017; Breck et al., 2019). Coyotes that are bolder and more curious are more likely to remain visible and engage with humans, unlike other wildlife, resulting in conflict.

Features of the Built Environment Used by Coyotes

Urban areas offer reliable and abundant resources that make the benefits of human development worth the associated risks for urban species such as coyotes, and these species will select developed areas over undeveloped land to use as corridors (Hansen et al., 2020; Oro et al., 2013; Way et al., 2004). Areas that coyotes take advantage of that offer the best of both the natural and manmade worlds include golf courses, train tracks, cemeteries, dumps, and roads (Tigas et al., 2002; Way et al., 2004; Way & Eatough, 2006; Wurth et al., 2020). Suburban development is commonly used by coyotes because it provides access both to anthropogenic food sources, and cover such as shrubs and trees (Ellington & Gehrt, 2019; Franckowiak et al., 2019; Murray & St. Clair, 2017; Way & Eatough, 2006). Coyotes will also take advantage of parks and other green spaces set aside within cities (Gámez & Harris, 2021). These land-use types highlight a compromise often made by urban coyotes—selecting for the least developed, developed land at the edge of human space.

Certain features of the built environment are likely important in determining which areas within cities coyotes choose to use to access anthropogenic resources. Identifying the particular features of human development that act as attractants and deterrents for coyotes is important to implementing successful strategies to reduce conflicts with humans. Limited research has examined the particular elements of urban areas that act as attractants or deterrents. However, Murray & St. Clair (2017) evaluated some fine-scale features and found that coyotes were less likely to enter backyards that had fences (Murray & St. Clair, 2017). Coyotes were more likely to access yards that had shrubs, accessible sheds and other forms of cover, as well as food sources such as bird seed and trash (Murray & St. Clair, 2017). They also observed that the presence of accessible fruit, such as berries or apples that had dropped to the ground, was a predictor of coyote visitation to a yard (Murray & St. Clair, 2017). Coyotes will repeatedly access a yard where they previously found food, showing that this species will learn that certain urban areas have high quality resources and return to them (Murray & St. Clair, 2017). While these studies offer a look into the specifics of what might draw coyotes to urban areas, they represent few in-depths investigations. More thorough research will need to be conducted to better ascertain specifically what is being selected for by urban coyotes.

Coyote use of developed areas—especially green spaces that are typically created explicitly for human use, could lead to more frequent conflict with humans. Any use by coyotes of space designed for humans will necessarily bring coyotes and people into contact as both species seek to exist in the same geographic area. This repeated selection for the same residential areas that contain certain features increases the chance that a coyote will eventually encounter the human who also uses that space. Thus, coyote appropriation of the built environment is likely a reason for increased reports of conflict in urban areas.

Diets of Urban Coyotes

The availability of anthropogenic food is a driver for animals to move into urban areas (Oro et al., 2013). Food resources are more readily available in urban areas, and this increase in reliable food can influence animals to select for areas of human development, even if there are other detracting factors (Howell, 1982; Oro et al., 2013). Coyotes in particular have much broader dietary requirements than similar species, such as bobcats that are considered to be strict carnivores, which allows them to take advantage of variation in resources across the urban landscape (Larson et al., 2015). Individual coyotes can also have very narrow diets, that differ from conspecifics, which allows them to subsist in varied habitats that might provide opportunities for specialists (Newsome et al., 2015). This wide variation in diets is likely a contributor to the success of coyotes in urban areas.

Coyote diets in cities differ from their more rural counterparts. Coyotes in more developed areas have higher percentages of human-related food sources in their diets (Morey et al., 2007). This food is accessed either when coyotes are fed directly by people or when they take advantage of things like pet food that are left outside (Baker & Timm, 2017). More broadly, in cities coyote diets are made up of rodents including mice and rats, fruit, non-native plants used in landscaping, as well anthropogenic items such as pet food and trash (Franckowiak et al., 2019; Morey et al., 2007; Poessel et al., 2017). Small mammals such as rabbits and mice are more common in more developed areas, so coyotes are likely taking advantage of residential areas to hunt, in addition to direct human sources of food (Way et al., 2004). In contrast, the diets of coyotes in rural areas consist of native plants, agricultural crops, and deer, with a lower percentage of small mammals and fruit (Morey et al., 2007; Poessel et al., 2017).

It is often speculated that human conflict with coyotes stems from predation of pets (Schmidt & Timm, 2007). However, most studies have found that domestic animals such as cats and dogs make up only a small proportion of coyote diets in cities (Morey et al., 2007; Poessel et al., 2017). While pets may not be a primary food source for coyotes, coyotes are more likely to abandon kills in urban areas in response to human disturbance, and therefore increase the amount of hunting activity needed for subsistence (Ellington & Gehrt, 2019). If coyotes include pets as a portion of their diet due to increased hunting activity, this could lead to an escalation in human-wildlife conflict.

Management Implications

Understanding what drives coyote success in cities is important for management considerations. However, given coyote adaptability in behavior, resource use, and diet, this management must focus on changes to human activity (Elliot et al., 2016). The work of Murray & St. Clair (2017) and future research can inform specific modifications to the built environment. One alteration that could be made is the addition of fences. Since fences are negatively correlated with coyote use of space, adding them may decrease interactions (Murray & St. Clair, 2017). Additionally, since coyotes are attracted to yards with fruit trees and shrubs, the removal of fruit that has fallen to the ground and trimming of shrubs may discourage coyote use of yards with those features (Murray & St. Clair, 2017). As coyotes shift to more nocturnal activity, humans can mitigate conflict by avoiding areas that coyotes utilize, such a green belts, during that time (Ellington et al., 2020; Way et al., 2004). Additionally, hazing—instead of apathy or even encouragement such as feeding, should be used to re-sensitize coyotes that exhibit bold behavioral traits (Bonnell & Breck, 2017; Breck et al., 2019). Decreasing coyote access to potential anthropogenic food sources such as those listed above would be helpful, but their broad and opportunistic diet presents a challenge, as any easily accessible source may be capitalized upon (Franckowiak et al., 2019). However, purposeful feeding of coyotes themselves should be strongly discouraged, and the removal of spaces that promote congregations of large numbers of small mammals like rats—such as open dumpsters, will limit this attraction. Most of these recommendations fundamentally involve educating the public about changes they can make to reduce conflict with coyotes (Bonnell & Breck, 2017).

Conclusion

So far, research into coyote use of urban areas has established that several factors contribute to this species' use of urban areas. Urban coyotes have a lower aversion to novel objects and human presence, which explains their willingness to spend time in cities and adapt to new conditions. As part of this behavioral change, coyotes are common in areas of human development, but show increased nocturnality. Elements of urban areas, such as shrubs and other human-related features, also facilitate this use. Understanding all of these factors is the first step in designing mitigation practices that can target human behavior and the built environment in order to reduce human-coyotes conflict. Despite the prevalence of conflict over several decades, many aspects of coyote use of urban areas are still not well understood, which contributes to the difficulty in effective management (Ellington & Gehrt, 2019; Grinder & Krausman, 2017; Howell, 1982; Tigas et al., 2002). In particular, more targeted research is needed on the specific elements of urban areas that attract or deter coyotes.

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CHAPTER 2. GRANT PROPOSAL

Investigating Attractants and Deterrents to Coyotes in The Urban Landscape

Abstract

In urban areas of North America coyotes (*Canis latrans)* have proven to be a particularly adaptable, and correspondingly difficult to manage, species. Coyotes are increasingly accounting for a large proportion of human-wildlife conflict. While research has looked at coyotes in urban areas at the broad scale, little has been done to investigate fine-scale features of the urban environment that are correlated with how coyotes use these spaces. To fill this knowledge gap, this study will look at the frequency of presence of coyotes in urban areas in response to aspects of the built environment such as pets, anthropogenic food sources, landscaping and fences. I will place trail cameras at study sites in Boulder County, Colorado. These sites will include residential yards, public, and commercial land that are confirmed to have features of interest. For residential yards, whether or not domestic dogs and cats are present will be recorded to look specifically at how this factor influences coyote use of those yards. Coyotes are commonly suspected to be involved in predation of pets and livestock. There is also an increasing concern about risk to human safety from coyote attacks. Therefore, understanding which features of the urban landscape coyotes avoid or are attracted to will inform management decisions regarding changes to the urban landscape that can deter this species from problem areas and improve human, domestic animal, and coyote wellbeing.

Anticipated Value

This study will inform management decisions that will reduce human-coyote (*Canis latrans*) conflict by providing data on aspects of the built environment that correlate with coyote presence. To understand how this species persists in cities it is necessary to isolate the specific elements that are associated with coyote presence in urban and residential areas. Few studies have been done to determine what specific local factors influence how coyotes move through urban areas. This study will evaluate such features to provide the basis for changes to the built environment and human behavior that deter coyote presence in problematic areas, ultimately protecting property and human and domestic animal welfare. Deterring coyotes from problem areas will also improve the wellbeing of coyotes themselves by reducing instances of disease transmission, vehicle collisions and attacks that may lead to lethal control. Additionally, this research expands knowledge about the behavioral ecology of this city-dwelling species and supports efforts towards understanding ways humans can co-exist with wildlife, especially large carnivores like coyotes.

Literature Review

Human-coyote interactions

As the largest frequently encountered wild carnivore in North America, coyotes are a common source of human-wildlife conflict. Over the last century coyotes have expanded into new geographic ranges, including into urban areas, leading to a documented increase in the frequency of negative interactions, such as depredation of pets and livestock and attacks on humans (Bateman & Fleming, 2012; Gehrt et al., 2011; Hody & Kays, 2018; Poessel et al., 2013). These interactions also have negative impacts on the coyotes such as increasing instances of vehicular collisions, dependence on anthropogenic food sources which can lead to disease transmission, and the triggering of lethal control measures (Baker & Timm, 2017; Oro et al., 2013; Way & Eatough, 2006). Behavioral adaptations and selective use of features of the built environment enable coyotes to be successful in urban habitat. Therefore, understanding how specific features of urban areas influence coyote presence and absence is the first step to mitigating conflict.

Behavioral adjustments to access anthropogenic resources

Coyotes in urban areas demonstrate an increase in bold and exploratory behavior that allows them to better access anthropogenic resources. Coyotes demonstrate bold behavior when they respond less dramatically to the presence of a potential threat, such as not fleeing when they encounter humans (Breck et al., 2019). Additionally, coyotes in urban areas show an increase in exploratory behavior, such that they are more likely to investigate new developments in their habitat (Breck et al., 2019). The tolerance of these animals to human activity and their willingness to explore new features of their environment make them more likely to find and take advantage of food and other resources found in urban areas (Breck et al., 2019; Schell et al., 2018).

Use of specific features in developed areas

Within urban areas coyotes make selections about which parts of the built environment to access. In particular, coyotes take advantage of spaces that provide access to both anthropogenic resources and natural areas or other cover that provides shelter (Ellington & Gehrt, 2019). Examples of these kinds of habitats include green spaces and railroad tracks which are commonly used as corridors between less developed areas, and golf courses which are frequented by coyotes when people are absent (Way & Eatough, 2006; Wurth et al., 2020). Cemeteries, suburban areas, and parks also provide much of this ideal pseudo-natural habitat for urban coyotes (Ellington & Gehrt, 2019; Franckowiak et al., 2019; Way & Eatough, 2006). Coyote use of these areas that are also heavily used by humans creates an opportunity for increased interactions and potential conflict.

Coyotes also seek out or avoid local areas of habitat based on the presence of certain factors. Human-related food sources such as accessible fruit from trees and bushes planted by people, bird feeders, and trash are positively associated with coyote presence (Murray & St. Clair, 2017). Cover such as sheds, accessible outbuildings and shrubs are also positively correlated with coyote selection of particular yards (Murray & St. Clair, 2017). Other common features that are associated with wildlife presence are gardens, compost piles, pet food and water sources (Hansen et al., 2020). Alternatively, fences are negatively associated with coyote presence, and may act as deterrents (Murray & St. Clair, 2017). Reports of depredation of pets and livestock suggest that the presence of domestic animals may also influence coyote use of human development (Baker & Timm, 2017; Wurth et al., 2020).

While previous studies have looked at overall movement patterns of coyotes in urban areas, little has been done to evaluate responses to individual elements of the built environment. Since fine scale variation within urban areas drives coyote selection of habitat, this study will identify these features to inform efforts aimed at reducing coyote presence and conflict with humans.

Objective

The objective of this study is to identify specific elements of urban areas that predict the presence of coyotes. I will quantify the influence of fences, shrubs, accessible outbuildings, water sources, pets, and other anthropogenic food sources such as pet food, trash and fruit trees by looking at percent cover and relative presence of these features. Additionally, I will assess the importance of each of these factors in driving coyote behavior by looking at frequency of coyote visitation where these factors exist, and quantifying which features are associated with the highest frequency of coyote visitation. This research will identify opportunities for modifications to the built environment and human behavior that will reduce human-coyote conflict.

Hypotheses 1

Coyote presence will increase in urban areas that contain features such as natural cover, man-made cover, and food sources such as pet food, water, trash and fruit trees, and will decrease in areas with fences and fewer sources of cover.

Hypothesis 2

Coyote presence will increase with the presence of domestic cats and dogs either because of the direct attractant of the pet, or because of the indirect effect of pet food.

Methods

Study Site Identification

To identify broad areas of coyote activity in Boulder County, I will collect sighting data from iNaturalist and reports from local animal management agencies to create a map of coyote presence. Once areas of general coyote presence are identified and mapped, I will assess the development and land cover types on both public and private property using GIS layers of land cover, tree canopy and wildland-urban interface classification (WUI). I will consider only developed areas—identified from the WUI layer from SILVAS lab as urban areas classified as "medium density" development or higher. National Land Cover Data from USGS will provide additional information on land cover type, canopy cover, and intensity of development to select local areas of focus for this study.

I will conduct visual surveys of urban areas that have established coyote presence to identify and verify the presence of natural cover, manmade cover, dumpsters, and fruit trees. These will be quantified using percent cover for trees and shrubs, and counts of dumpsters, sheds, fruit trees and fences each site. I will conduct community outreach, including door-to-door surveys, with residents of identified study areas to assess presence of pets. For private residences I will record whether or not domestic dogs or cats are present. Once locations of properties with pets, natural or manmade cover, trash or fruit trees have been identified, I will obtain permission from private residents, commercial or governmental owners to access properties to place cameras. A total of 30 camera sites will be randomly selected from identified properties of interest.

Analysis

I will check cameras weekly over a 3-month period. For each week the number of sightings of coyotes—defined as photos taken more than 30 minutes apart, will be calculated as sightings per week. I will create a linear model in R (R Core Team, 2018), comparing the number of sightings per week against values for features of interest, such as percent cover or number of dumpsters, to assess differences in mean number of sightings as a function of the presence of fences, shrubs and trees, sheds, pets, trash, and fruit trees. Additionally, I will conduct an ANOVA to compare coyote sightings per week with the presence or absence of pets. Only data from private residences for which the presence or absence of a domestic dog or cat can be confirmed will be used to test this hypothesis.

Negative Consequences

Limited risk exists to natural resources for this study. Cameras will be placed in temporary locations with no harm to any natural resources. Passive observation through the cameras should offer minimal disruption to wildlife.

Schedule

March through Mid-April 2022	Conduct GIS analysis, visual survey and community outreach
Mid-April through May 2022	Obtain permission for access to selected sites
June through August 2022	Check camera traps weekly
September through Mid-October 2022	Conduct data analysis and assemble report
Late October 2022	Draft Final Report Submitted
Early December 2022	Final Report Submitted

Budget

Item	**Cost**			**Justification**
	Cost/item	Quantity	Total	
Trail Cameras (*Bushnell* Core DS No Glow – 30MP)	$220	30	$6600	Cameras selected for pixel quality and no glow feature. One per site.
SD cards (*SanDisk*, 32 GB)	$12	60	$720	32GB for storage for 1 week of photos. 2 per site, trade weekly.
Rechargeable batteries (*Energizer*, AA)	$3	360	$1080	2 sets of 6 batteries per camera/site, trade weekly.
Battery Charger	$15	7	$105	Enough chargers to charge whole set of batteries each week.
Field Assistant	$15	99 hours	$1485	Assistant to help with community surveys and checking of camera traps.
Total			**$9990**	

Qualifications of Researcher

Chelsea Elizabeth Huck Chelsea.Huck@gmail.com
720-934-8362

EDUCATION

Masters of Science in Environmental Biology, Regis University, Denver, Colorado May 2022

Coursework at Metropolitan State University of Denver 2016-2021
Biology, Chemistry, Mathematics GPA 4.0

B.A. Communication, Minor in Anthropology, University of Colorado Denver May 2013
Dean's List, Graduated Cum Laude GPA 3.9

RESEARCH EXPERIENCE

Springsnail Gene Sequencing, Metropolitan State University of Denver 2019-2020

- DNA extraction on invertebrate specimens
- Polymerase Chain Reaction amplification, and preparation of samples for sequencing
- Edited and aligned sequences using Sequencher and MegaX, and referenced using Nucleotide BLAST

Black-tailed prairie dog vigilance in an urban colony, Metropolitan State University of Denver 2019

- Scan sampling of multiple individuals
- Coded behavior as “vigilant” or “non-vigilant”
- Analyzed significance using statistical tests

RELEVANT ACADEMIC PROJECTS

Great Blue Heron habitat suitability in metro Denver 2020

- GIS analysis of Great Blue Heron habitat along the South Platte in Denver
- Created maps showing possible habit opportunities and constraints
- Used maps to determine locations of possible Great Blue Heron habitat in greatest need of remediation and conservation

Using crowd-sourced data to evaluate bird density predictors 2021

- Analysis of passerine density in Colorado using GIS and data from eBird and iNaturalist
- Ran regression models in GeoDa to determine significance

PRESENTATIONS AND CONFERENCES

Undergraduate Research Conference Metropolitan State University of Denver April 2020
Sequencing of 16S, 18S, and 28S Genes to Clarify *Fontigens* Phylogeny Poster Presentation

SOFTWARE, TECHNICAL AND LABORATORY SKILLS

ArcGIS Pro
Adobe Creative Suite
Microsoft Office Suite
ENVI
R
Sequencher
MegaX
DNA extraction
PCR
Gel electrophoresis

PROFESSIONAL EXPERIENCE

Public Services Associate, Standley Lake Public Library 2014-2021

- Compiled statistics, reviewed and verified data, appropriately classified new and recurring data
- Managed patron records with a high degree of accuracy and attention to detail while preserving confidentiality
- Created daily, weekly, and monthly schedules for a staff of 15
- Planned and presented STEM programming
- Coordinated internal and public events and programs
- Conducted outreach activities to public groups and other organizations in the community
- Designed and managed a system for processing and tracking purchase requests, orders, and invoices
- Reconciled receipts and investigated discrepancies in cash drawer and weekly deposit

Reference and Government Publications Assistant, Auraria Campus Library 2011-2014

- Used databases to manage electronic and paper records and process materials
- Received and processed new books, maps, and other materials for integration into collection
- Responded to requests for materials and carried out accurate and timely routing procedures

Teaching Assistant, Girls Inc. of Metro Denver 2012

- Created lesson plans and presented educational programming
- Arranged fieldtrips and special events for participants

Registration Assistant, University of Wyoming Art Museum 2009-2010

- Conducted inventory of artwork
- Performed general office and administrative tasks
- Maintained clerical and statistical records through accurate data entry and filing of documents
- Set up and staffed special events

Appendix: Map of Study Area

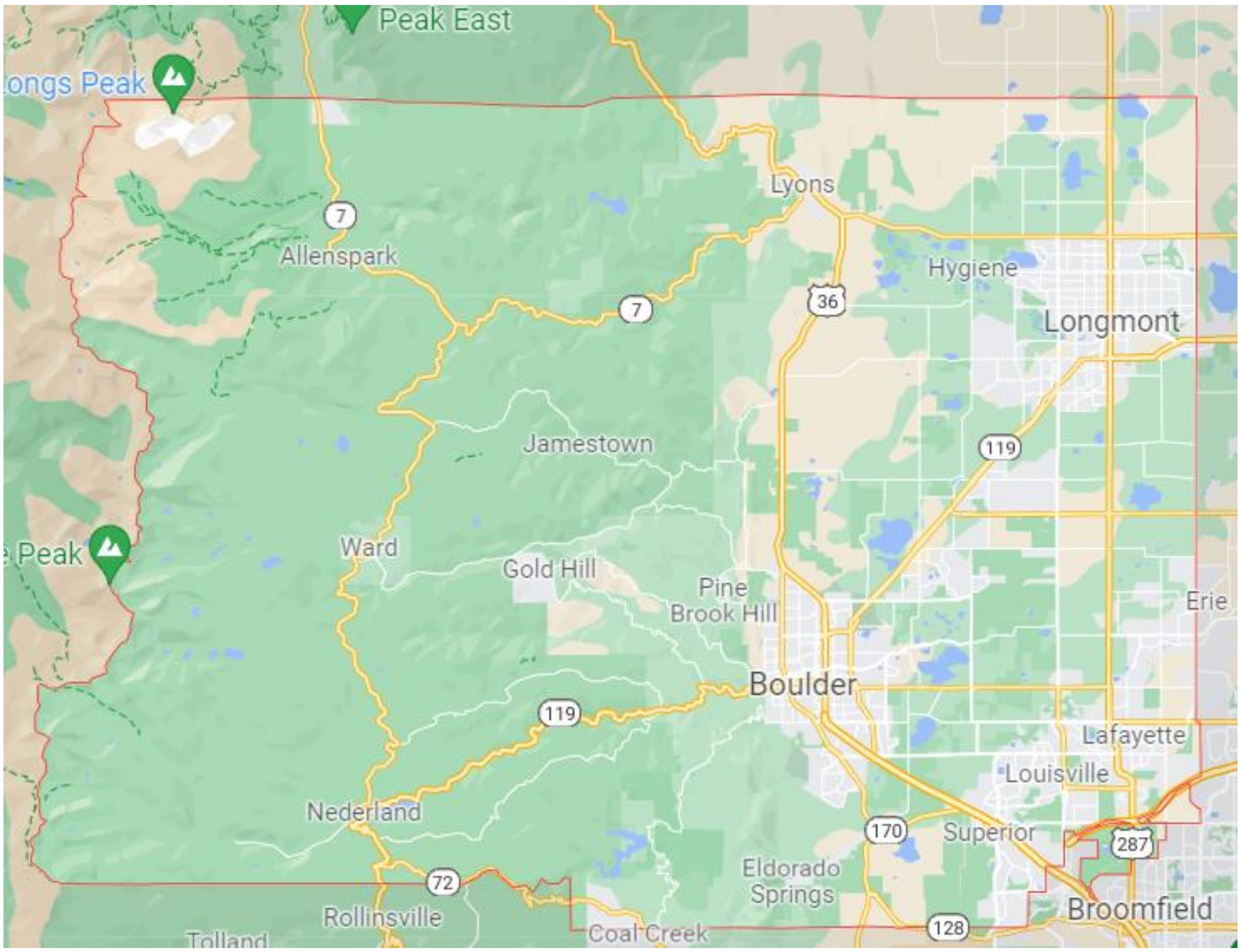

Figure 1 Map of overall study area, within which areas of coyote presence and human development will be identified (Google Maps, 2021).

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CHAPTER 3. JOURNAL MANUSCRIPT

Bull Asian Elephants at Denver Zoo Engage in Less Daytime and Nighttime Stereotypy When Housed Socially Compared to When Housed Alone

Abstract

Zoological institutions, as part of their mission to protect species in the wild, place enormous emphasis on understanding and enhancing the well-being of animals in their care. Engagement in stereotypic behavior is commonly assessed to find possible areas for improvement of welfare, and is a principal concern in and of itself. Asian elephants (*Elephas maximus)* are a common species in zoos and are more prone to stereotypy than their African cousins. Despite the prevalence of elephants in managed care, a gap persists in the understanding of nighttime behavior, especially of bull elephants in groups. Our study evaluated the effect of social housing on stereotypic behavior in five bull Asian elephants at Denver Zoo, during both the day and night. We observed elephants alone and in social groupings and recorded behaviors at one-minute intervals over 30-minute samples throughout the day. We then used generalized linear models to determine whether social housing was correlated with the proportion of time elephants engaged in stereotypy. We found that social housing was associated with a significant reduction in the odds of an elephant engaging in stereotypic behavior, at all times of day. We also found that variation in stereotypy between individuals was important at all times, and that the total area to which elephants had access was related to stereotypic behavior during the day. This suggests that social housing throughout the day and night improves bull elephant welfare, and we encourage exploration of this relationship further in this species, as well as other social animals.

Introduction

Maintaining the welfare of animals in managed care is a top priority for zoological institutions. In the last few decades much work has focused on determining the best ways to assess and maintain the health of animals in human care (Brando & Buchanan-Smith, 2018; Greco et al., 2016a; Swaisgood & Shepherdson, 2005). Assessing welfare often revolves around three aspects of an animal's life: how much of its existence resembles its natural life history, its mental and emotional well-being, and its physical health (Brando & Buchanan-Smith, 2018). To ensure these needs are met, managers generally monitor behavior, in addition to physiological functions (Meehan et al., 2016).

In particular, persistent stereotypic behavior suggests poor animal welfare and often co-occurs with other indicators and causes of inadequate environments (Greco et al., 2016b; Sherwen & Hemsworth, 2019). Stereotypic behaviors are repeated, continuous actions that do not seem to achieve any specific goal or function (Swaisgood & Shepherdson, 2005). Stereotypy is often associated with feeding schedules and social structures that differ from natural settings, particularly predictability in daily routines, and a lack of stimulation in animals' environments (Brando & Buchanan-Smith, 2018; Greco et al., 2016b; Swaisgood & Shepherdson, 2006). Current stereotypic behavior can also be a result of previous poor environments (Swaisgood & Shepherdson, 2005), and as such is often a lifelong concern for animals, even if their overall welfare improves.

Monitoring stereotypy is especially important for large animals that would have correspondingly large home ranges in the wild and that have complex social behaviors, such as elephants (Greco et al., 2017; Swaisgood & Shepherdson, 2005). Both Asian (*Elephas maximus*) and African (*Loxodonta Africana*) elephants are commonly featured in zoos and similar institutions around the world (Lukacs et al., 2016). In the wild the social structure of elephants is often complex, involving large, multigenerational groups that routinely travel enormous distances (Byrne et al., 2009). Elephant cognitive ability is demonstrated by large brains relative to their body size, tool use, and the ability to maintain large home ranges and social relationships (Byrne et al., 2009; Hart et al., 2001; Williams et al., 2019). This complex sociality, paired with their high level of intelligence, makes meeting elephants' mental and physical needs both essential and a challenge in managed care. Managers commonly assess stereotypy to gauge elephant welfare, and Asian elephants, more so than African elephants, are prone to stereotypic behaviors (Meehan et al., 2016). Common categories of stereotypy in elephants include oral, locomotor, and repetitive movement, including pacing and body-swaying (Greco et al., 2017; Meehan et al., 2016; Rees, 2009).

While stereotypy has been studied in Asian elephants broadly (Greco et al., 2016b; Greco et al., 2017; Meehan et al., 2016; Readyhough et al., 2022; Rees, 2009), research that focuses on bull elephants is less common (but see Readyhough et al., 2022; Schreier et al., 2021). Historically, bull Asian elephants were thought to be largely solitary, but recent studies show that like their female counterparts, males also engage in social relationships with conspecifics (de Silva & Wittemyer, 2012; Hartley et al., 2019; Schreier et al., 2021; Thevarajah et al., 2021). Bull elephants interact socially for play and to learn appropriate behaviors (Goldenberg et al., 2014; Lee & Moss, 2014). Despite this recent expansion of knowledge, the implications of this sociality on the welfare of male elephants in managed care has rarely been studied (Hartley et al., 2019; Posta et al., 2013; Schreier et al., 2021; Thevarajah et al., 2021). This lack of research is due in part to the large size of bull elephants and hormonal cycles that make housing multiple individuals together in human care challenging and potentially dangerous (Hartley et al., 2019).

However, research so far has found that housing bull elephants socially may increase well-being (Chiyo et al., 2011; Schreier et al., 2021).

Most studies focus only on daytime elephant behavior, but since nighttime activity makes up roughly half of the daily activity budget for elephants, this leaves a large amount of time for which little is known about elephant social and stereotypic behavior. Greco et al. (2016b) assessed elephant behavior at night, but most elephants included in the study were female. Readyhough et al. (2022) studied a group of bull elephants and found a decrease in stereotypy when elephants were housed socially but did not look at nighttime behavior specifically. Thevarajah et al. (2021) looked at a bachelor group of Asian elephants at night and found that levels of activity were influenced by social conditions, with bulls in new social groups resting less than those in established pairs, suggesting that nighttime behavior and social interactions warrant closer attention. Despite this recent work, a dearth of knowledge still exists and an assessment of stereotypy in bull elephants in relation to both social housing and time of day is needed to fill this substantial gap (Greco et al., 2016b).

As one of few zoos in the world to house multiple bull elephants together during both the day and night (Hartley et al., 2019; Schreier et al., 2021), Denver Zoo provides a unique opportunity to study how social housing influences stereotypic behavior in males of this species. Denver Zoo in Denver, Colorado houses a group of five male Asian elephants (*Elephas maximus*) aged 11, 15, 49, 10, and 9 at the start of the study (referred to as individuals 1-5, respectively).

In this study, we focus on the bachelor group at Denver Zoo to evaluate how social housing and time of day influence bull elephant engagement in stereotypic behaviors. First, we hypothesize that elephants will engage in stereotypy more when they are housed alone compared to when they are housed with a conspecific, due to the lack of stimulation from interaction with another elephant. Specifically, we predict that elephants will spend a greater proportion of scans in stereotypy when they are housed alone than when with another elephant, both during the day and at night. We also hypothesize that time of day will affect engagement in stereotypy and predict the magnitude of the effect of social housing will be larger during the day than at night because elephants are less active overall at night. Investigating these hypotheses will contribute to the scant knowledge about how sociality in bull elephants is related to welfare, particularly at night, and inform better management practices for this species.

Methods

Study species

We observed bull Asian elephants housed at Denver Zoo in Denver, Colorado. The elephant enclosure at the zoo totals 2.7 acres and is composed of five outdoor yards, an indoor parlor, and several indoor stalls. Throughout the day and night elephants have access to varied combinations of indoor and outdoor spaces and are housed in groups of different sizes from individually up to all five together. Cameras equipped with infrared record continuously through the elephant habitat, with two or three views of a given area at a time.

Data Collection

We conducted instantaneous scan sampling on focal elephants across 30-minute samples, recording data at 1-minute intervals while elephants were housed both alone and socially. At each interval we recorded the behavior of animals using behaviors as defined in a pre-constructed ethogram or as “out of view”. Stereotypic behaviors were recorded as “pace” or “head-bob” (Table 1). We recorded all behavior observations in ZooMonitor (Ross et al., 2016). We collected nighttime observations from 6:00pm to 6:00am using videos recorded between

February 2019 and January 2020, and we collected daytime observations between 9:30am and 11:30am and 1:30pm to 3:30pm between August 2018 and December 2019. This resulted in a total of 1,194 hours of observations, 481 hours of observation during the day and 713 hours at night. Of those observations, 218 hours observed solo elephants and 976 hours socially housed elephants. Solo elephants were observed for 85 hours at night, and social groupings for 268 hours. During the day social groupings were observed for 348 hours and solo elephants for 133 hours.

Table 1. Ethogram of behaviors for bachelor group of five bull Asian elephants at Denver Zoo.

Behavior Category		Behavior	Definition
Agonistic	**Non-Contact**	Approach head high	Actor moves toward recipient to within two body lengths with head above shoulders and ears out perpendicular
		Charge	Rapid forward lunging or rapid gait by actor towards a stationary conspecific starting from more than two body lengths away
		Chase	Actor rapidly pursues recipient, who is moving away from actor, for at least 5 seconds
		Head shake	Actor holds head above shoulders and moves vigorously from side to side, up and down, or in circular motion
		Supplant	Actor approaches to within two body lengths of conspecific without making contact, causing recipient to turn away or yield ground
	Contact	Grasp tail	Actor places tail of conspecific into its own trunk while recipient attempts to move away from focal animal
		Kick	Actor strikes at recipient with rear limb
		Mount	Actor rears up on hind legs and places forelegs on recipient for 5 seconds or more
		Push	Actor contacts conspecific with enough force to displace recipient
		Spar	Two elephants mutually and simultaneously push one another backwards with force with heads and/or heads and trunks and this is sustained for at least 5 seconds
		Trunk over back	Actor places 2/3 or more of its trunk firmly over the back or head of a conspecific

Affiliative	Approach relaxed	Actor moves to within to within two body lengths of recipient with head low and ears lying flat against its head, not associated with any other behavior
	Body contact	Body contact unspecified in any other behavior (e.g., side-to-side rubbing or touching)
	Play	Actor voluntarily spars, wrestles with, mounts, or chases recipient without obvious intent to do harm or display dominance or for less than 5 seconds; does not include when following agonistic interaction
	Shares food/object	Actor either feeds or uses an object in concert with another elephant that is within one body length
	Trunk tangle	Actor loosely entwines its trunk with that of recipient
	Trunk to mouth	Actor places its trunk in another elephant's mouth
	Trunk touch/toward	Actor extends trunk toward recipient with or without touching; not associated with any other behavior
Submissive	Allow	Actor remains still and calmly permits physical contact by conspecific, including genital investigation
	Back into/toward	Actor takes two steps (minimum) backward towards another elephant to within one body length, with or without touching
	Lower head or ears	Actor quickly drops head and/or ears in response to approach by another elephant
	Run away	Actor flees from conspecific in response to its agonistic contact, display, or approach
	Turn away/yield	Actor turns body away from or yields ground as a result of actions or encroachment by another elephant
Other	Bathe/swim	Actor lies, stands, or submerges in pool (includes spraying water on self); not associated with any other ethogram behavior
	Drink	Actor uses trunk to bring water to its mouth and drink
	Dust/mud	Actor uses trunk to throw dirt, sand, shavings, or mud onto body while standing
	Enrichment interaction	Actor interacts with provided non-food enrichment items
	Feed	Actor ingests presented diet items; includes manipulating food items
	Follow	Actor closely trails behind recipient, who is moving away from actor (at normal walking speed)

	Genital investigation	Actor sniffs or touches genitals of another elephant with its trunk
	Locomotion	Actor moves directionally along a horizontal surface (not while feeding); can include slow or fast walking or running
	Rest	Stationary; lying down or standing with trunk resting loosely on the ground; eyes open or closed; not performing any other behavior
	Head-bob	Actor displays repetitive head rotation/movement from side to side, at least two repetitions within 10 seconds
	Pace	Actor repeatedly walks the same line of travel, at least three times
	Wallow	Actor lies or rolls in mud or dirt
	Other	Actor performs any behavior not on ethogram
Out of View	Out of view	Actor cannot be seen or cannot be distinguished from other elephants

Data analysis

Effect of social housing

To investigate the hypothesis that elephants engage in more stereotypy when they are housed alone compared to when they are housed with conspecifics, we fit a generalized linear model (GLM) using the proportion of scans spent in stereotypy as the response, on observations from both daytime and nighttime. These models used social housing as the primary predictor as well as several additional variables as fixed effects (Table 2). After fitting a full model, we removed non-significant variables and used a drop-in deviance test to assess the fit of the reduced model.

Table 2. Description of variables considered in Generalized Linear Models.

Variable	Description	Reference Level
StereoProp	Numeric (binomial proportion) variable indicating proportion of scans that the focal animal was engaging in stereotypy (x/30)	NA- response variable
Socialized	Binary variable indicating if the focal animal was housed alone (0) or with at least one conspecific (1)	Alone (0)
AccessArea	Continuous variable indicating the size of the area that the focal animal had access to (per 1,000 ft^2); 2.00-47.37	2,000 ft^2
InOutAccess	Categorical variable indicating if focal animal had access inside (in), outside (out), or both (both)	Both
DayNight	Binary variable indicating if observations took place in the Night (1) or Day (0)	Day (0)
InOutAccess*AccessArea	Interaction term between InOutAccess (in, out, both) and AccessArea (2.00-47.37)	Both:AccessArea
FocalName	Categorical variable indicating the name of the focal animal being observed (Bodhi A11292, Groucho A12007, Billy A13125, Chuck A18202, Jake A18203, UNK 1, UNK 2)	NA
NewSocial	Binary variable indicating whether the social group was new (1) or established (0)	Established (0)

Effect of time of day

To compare the influence of time of day on proportions of stereotypy we fit two additional binomial GLMs, one using just daytime and one just nighttime observations. These models used the same fixed effects as the initial models (Table 2), but the nighttime model looked only at three individuals that engaged in stereotypy at night. After fitting each full model, we removed non-significant variables and used a drop-in deviance test used to assess the fit of the reduced model. We performed all data analysis in R v4.0 (R Core Team, 2021). To investigate differences in the effect of social housing on stereotypy between day and night we compared differences in odds and the overlap between confidence intervals.

Results

Effect of social housing

Regardless of time of day, socially housed bull elephants spent significantly less time engaged in stereotypy than elephants housed alone. When data from both day and night were pooled, elephants spent a lower percentage of scans engaging in stereotypy when housed socially (0.25% of scans, 95% CI: 0.02 to 0.49%, Figure 1), as opposed to when they were housed alone (6.00% of scans, 95% CI: 3.71 to 8.30%, Figure 1). The best model assessing the effect of social housing on stereotypy for these data also included the focal individual as a fixed effect (Table 3). This model indicated a statistically significant 94.33% decrease in the odds of engaging in stereotypy when housed socially, as opposed to alone (95% CI: 83.95 to 98.00% decrease, p-value<0.05, Table 4).

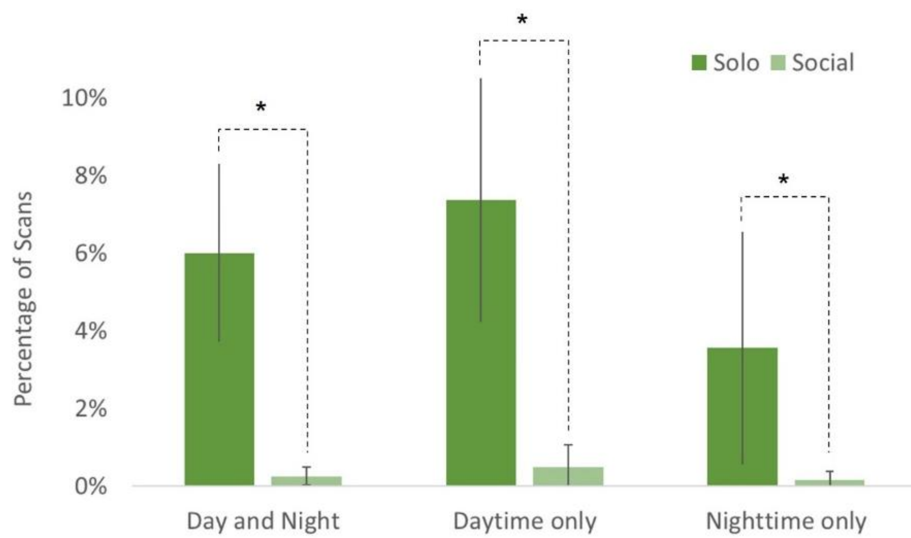

Figure 1 Differences in the proportion of scans engaged in stereotypy when housed socially or alone. * Indicate significance (p-value<0.05).

Individual elephants also spent different amounts of time engaged in stereotypy. Individual 5 did not engage in stereotypic behavior during the study, while individuals 1, 2, 3, and 4 engaged in stereotypy in 0.41% (2.02% when solo and 0.008% when socially housed), 2.41% (10.16% solo and 0.45% when social), 4.63% (11.00% solo and 1.03% social), and 0.89% (4.69% solo and 0.26% social) of scans, respectively.

Table 3. Comparison of Generalized Linear Models with stereotypy as the response on all data, just daytime data, and just nighttime data. P-value from drop-in-deviance test assessing performance of the reduced model against the full model. Insignificant p-value (>.05) indicates model performs as well with reduced parameters. Final models in bold.

All Data Model			
Fixed Effects	AIC	p-value	Number of parameters
*Socialized + DayNight + InOutAccess + AccessArea + NewSocial+(InOutAccess * AccessArea) + FocalName*	179.6	-	7
*Socialized + DayNight + InOutAccess + AccessArea + (InOutAccess * AccessArea)+ FocalName*	177.6	0.95	6
Socialized + DayNight +InOutAccess + AccessArea + FocalName	177.5	0.51	5
Socialized + InOutAccess + AccessArea + FocalName	176.9	0.58	4
Socialized + AccessArea + FocalName	175.5	0.42	3
Socialized + FocalName	**173.7**	**0.52**	**2**
Daytime Only Model			
Fixed Effects	AIC	p-value	Number of parameters
*Socialized + InOutAccess + AccessArea + NewSocial + (InOutAccess * AccessArea) + FocalName*	142.3	-	6
Socialized + InOutAccess + NewSocial+ AccessArea +FocalName	144.4	0.12	5
Socialized + NewSocial + AccessArea +FocalName	141.4	0.15	4
Socialized + AccessArea + FocalName	**139.9**	**0.32**	**3**
Nighttime Only Model			
Fixed Effects	AIC	p-value	Number of parameters
*Socialized + InOutAccess + AccessArea + NewSocial + (InOutAccess * AccessArea) + FocalName*	43.2	-	6
Socialized + InOutAccess + AccessArea + NewSocial + FocalName	40.5	0.17	5
Socialized + InOutAccess + AccessArea + FocalName	38.5	0.13	4
Socialized + AccessArea + FocalName	34.8	0.29	3
Socialized + FocalName	**33.5**	**0.34**	**2**

Table 4. Results of the best fitting generalized linear model on pooled daytime and nighttime data. ß = Beta coefficients from model outputs: positive values indicate an increase in odds compared to the reference level while negative values indicate a decrease in odds compared to reference level; SE = standard error of beta coefficients, p and z values from t-test. * indicates <.05 statistical significance.

Predictor	Odds Ratio	ß	SE	z-value	p-value	
FocalNameBilly A13125	0.02	-4.00	0.68	5.87	0.00	*
FocalNameBodhi A11292	5.96	1.79	0.75	2.38	0.02	
FocalNameChuck A18202	0.00	-15.69	1249.91	-0.01	0.99	
FocalNameGroucho A12007	7.26	1.98	0.74	2.68	0.01	*
FocalNameJake A18203	2.74	1.01	0.83	1.22	0.22	
FocalNameUNK 1	0.00	-14.70	4310.09	0.00	1.00	
FocalNameUNK 2	0.00	-14.70	4310.09	0.00	1.00	
Socialized	0.06	-2.87	0.53	-5.40	0.00	*

Effect of time of day

This relationship between social housing and stereotypy was also clear when elephants were observed just during the day. During the day elephants spent a lower proportion of scans engaging in stereotypy when housed socially (0.48%, 95% CI: -0.10 to 1.05%, opposed to 7.36%, 95% CI: 4.22 to 10.50%) during the day, Figure 1). The best model evaluating stereotypic behavior during the day also included focal individual and total access area as fixed effects (Table 3). This model showed a significant 86.83% decrease in the odds of elephants engaging in stereotypy during the day when housed socially while accounting for focal individual and area to which the elephant had access (95% CI: 45.49% to 96.81% decrease, p-value<0.05, Table 5).

Table 5. Results of the best fitting generalized linear model on just daytime data. ß = Beta coefficients from model outputs: positive values indicate an increase in odds compared to the reference level while negative values indicate a decrease in odds compared to reference level; SE = standard error of beta coefficients, p and z values from t-test. * indicate <.05 statistical significance.

Predictor	Odds Ratio	ß	SE	z-value	p-value	
FocalNameBilly A13125	0.06	-2.86	0.77	-3.72	0.00	*
FocalNameBodhi A11292	3.76	1.32	0.79	1.68	0.09	
FocalNameChuck A18202	0.00	-15.64	1276.79	-0.01	0.99	
FocalNameGroucho A12007	5.43	1.69	0.76	2.22	0.03	*
FocalNameJake A18203	1.85	0.61	0.95	0.65	0.52	
Socialized	0.13	-2.03	0.72	-2.80	0.01	*
AccessArea	0.94	-0.06	0.04	-1.68	0.09	

During nighttime elephants also spent a lower proportion of scans engaging in stereotypy when housed alone versus with a conspecific. At night elephants spent 0.15% (95% CI: 0.0 to 0.37%) of scans engaged in stereotypy when housed socially and 3.56% (95% CI: 0.56 to 6.56%) of scans engaged in stereotypy when housed alone. The best model including stereotypic behavior just at night also included focal individual as a fixed effect, and only included the three individuals that engaged in stereotypy at night (Table 3). This model showed a significant 95.67% decrease in the odds of elephants engaging in stereotypy during the night when housed socially while accounting for the focal individual (95% CI: 75.25% to 99.24% decrease, p-value<<<.05, Table 6).

The magnitude of the reduction in the odds of stereotypic behavior when elephants were housed socially at night was greater (95.67% decrease) than the corresponding reduction during the day (86.83%). However, the 95% confidence intervals overlapped substantially (daytime

45.49% to 96.81% and nighttime 75.25 to 99.24%), indicating that this response was largely consistent regardless of the time of day.

Table 6. Results of the best fitting generalized linear model on just nighttime data. ß = Beta coefficients from model outputs: positive values indicate an increase in odds compared to the reference level while negative values indicate a decrease in odds compared to reference level; SE = standard error of beta coefficients, p and z values from t-test. * indicate <.05 statistical significance.

Predictor	**Odds Ratio**	**ß**	**SE**	**z-value**	**p-value**	
FocalNameBodhi A11292	0.11	-2.21	0.65	-3.38	0.00	*
FocalNameGroucho A12007	1.09	0.09	0.95	0.09	0.93	
FocalNameJake A18203	0.33	-1.10	0.95	-1.16	0.25	
Socialized	0.04	-3.14	0.89	-3.53	0.00	*

Discussion

The goal of this study was to determine the role that social housing plays in the welfare of bull elephants in human care. Research on bull elephant social behavior in managed care is limited due to challenges associated with housing multiple male elephants together (Hartley et al., 2019). However, recent work shows that male elephants have rich social lives (Schreier et al., 2021; Thevarajah et al., 2021) and may benefit from social housing (Readyhough et al., 2022). Information on nighttime behavior in elephants in general, and bulls in particular, is also limited (Thevarajah et al., 2021), so this study contributes to the resolution of an existing knowledge gap by examining bull elephant behavior at night. As predicted, the bull elephants at Denver Zoo spent significantly less time across both day and night engaged in stereotypy when they were housed with another elephant than when they were alone. This decrease in the odds of stereotypic behavior was consistent regardless of time of day. There is some indication that the drop is more pronounced at night, contrary to our prediction, but the larger magnitude of change at night was not significant, with confidence intervals that overlapped almost entirely with the change in odds during the daytime.

Social housing and focal individual were the variables that significantly predicted odds of engaging in stereotypy across all time periods. This shows that social interactions are especially important to elephant welfare, even compared to other factors that may influence stereotypy such as length of social relationship and access to the outdoors. Total access area was also marginally significant during the daytime. Decreases in the total area to which an animal has access is associated with an increase in stereotypic behavior in other large animals (Hogan et al., 1988), so the influence of access area is not unexpected. Research on elephants specifically shows that the amount of space that elephants have access to is important for their welfare overall as part of maintaining social hierarchies, engagement in physical activity, and other enrichment (Hartley et al., 2019; Koyama et al., 2012; Meehan et al., 2016; Schreier et al., 2021). The importance of access area may have been clearer during the day because elephants engage in more activity overall during the day, and therefore may utilize their space more extensively at this time than at night (Greco et al., 2016b; Posta et al., 2013).

Frequency of stereotypy varied across individuals. The oldest elephant in the group engaged in the behavior nearly twice as often as any other individual and the youngest individual did not engage in stereotypy at all during our observations. Stereotypic behavior persists beyond the initial conditions that may have led an animal to developing it (Mason et al., 2007; Swaisgood & Shepherdson, 2005), and age and the number of times an elephant has moved between institutions influence the likelihood of an elephant engaging in stereotypy (Greco et al., 2006b; Meehan et al., 2016). Thus, it is likely that differences in the life history between the youngest and oldest individuals in this group influence the degree to which they display stereotypy. This finding suggests that stereotypy and the associated welfare concerns require attention at the level of individual animals.

The reduction in stereotypy we observed when elephants were housed socially is in-line with previous research showing the importance of social interactions for elephants (Gruber et al., 2000). Elephants in managed care that are kept isolated from conspecifics display increased stereotypic behaviors (Greco et al., 2016b; Kurt & Garai, 2001), suggesting a strong inverse relationship between sociability and stereotypy. Stereotypic behaviors are also more common when the routines of elephants are predictable and/or different from what they would experience in the wild (Brando & Buchanan-Smith, 2018; Swaisgood & Shepherdson, 2006). Therefore, our observation of engagement in less stereotypy when housed with a conspecific could be a direct result of comfort from another elephant and social interactions that more closely resemble their natural environment (Rees, 2009; Swaisgood & Shepherdson, 2006).

Despite the long-held assumption that bull elephants are solitary, recent evidence shows that in the wild male elephants maintain social relationships similar to their female counterparts (Lee & Moss, 2014; Schreier et al., 2021; Thevarajah et al., 2021). The finding here that shared housing with a conspecific reduces stereotypy supports the growing evidence that bull elephants in human care benefit from social housing. However, most bull elephants in zoos are not commonly housed in social groups (Hartley et al., 2019; Schreier et al., 2021). Thus, while there are risks associated with housing multiple bulls together and costs to constructing sufficient infrastructure (Hartley et al., 2019), housing bull elephants together both during the day and at night improves their welfare significantly and is worth the time and effort to arrange where possible for animals in managed care.

The gap in knowledge about elephant behavior at night has persisted despite the importance of nighttime behavior to welfare (Horback et al., 2014; Thevarajah et al., 2021) and the fact that elephants in managed care are often kept in their nighttime housing for longer than elephants in the wild would be resting overnight due to care staff schedules (Greco et al., 2016b). This study contributes to filling this gap. Our finding that social housing at night results in a reduction of stereotypic behavior reinforces the importance of considering the sociality of bull elephants at night, as well as during the day.

Stereotypic behavior is linked to negative physical and psychological conditions (Kurt & Garai, 2001; Mason et al., 2007), so limiting its occurrence is essential to providing good quality of life for animals in human care. Engagement with enrichment is a positive welfare behavior and has been observed to reduce stereotypy (Greco et al., 2016a; Mason et al., 2007; Meehan et al., 201; Swaisgood & Shepherdson, 2006). Previous work suggests that social housing may provide an additional form of enrichment for elephants (Rees, 2000; Rees, 2009). Our observation that socially housed elephants engage in stereotypy less frequently than when they are housed alone supports the idea that social interactions are providing an alternative form of stimulation for the elephants. Thus, exploring the relationship between enrichment, stereotypy, and social housing is a promising avenue for future research.

The findings of this study are limited by the number of elephants in the bachelor group we observed. Only four of the five elephants in our study displayed stereotypic behavior, which means individual variation in behavior likely influenced the observed differences. Individual number 1 also did not engage in stereotypy overnight, which may make individual differences even more stark in that dataset. A larger sample size of elephants could provide stronger evidence for the relationship between stereotypy and social housing at a broader scale. We were also limited by the greater amount of data available at night and from socially housed elephants. A more equal distribution of data may provide more robust results and future studies should look at data on stereotypic behavior in larger groups of elephants, which would be less influenced by individual differences. Despite these limitations, the findings of this study were significant and the observation of reduced stereotypic behavior when housed socially would likely remain clear when these factors are accounted for. Future work should also explore the relationship between stereotypy and other welfare-related behaviors and whether the size of herds is related to the benefit of social housing.

Ensuring that animals in human care maintain a good quality of life is a top priority for zoological institutions. This is especially important for social species such as elephants for whom social interactions would occur in natural environments (Mallapur, 2009; Massen et al., 2010; Schreier et al., 2021). Given the negative association between stereotypy and welfare (Greco et al., 2016b; Kurt & Garai, 2001; Mason et al., 2007; Sherwen & Hemsworth, 2019), our finding that social housing at night reduces stereotypic behavior reinforces the need to make social housing a primary consideration for other social species in zoos.

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CHAPTER 4

Mitigating Wolf-Human Conflict Through Cooperation, Education, and Planning

Introduction

Gray wolves (*Canis lupus*) lived in what is now known as Colorado for thousands of years before the arrival of white colonizers (Coleman, 2004; Smith & Peterson, 2021). But by the early 20th-century loss of prey and habitat from human activity, as well as the direct killing of wolves, had forced them from both Colorado and most of the contiguous United States (Bergstrom et al., 2009). Since the passing of the Endangered Species Act (ESA) in 1973, and the subsequent listing of the gray wolf as endangered, reintroduction efforts have taken place around the country (Bergstrom et al., 2009). Wolf populations were less severely reduced in Canada, and in the 1980s individuals from packs north of the border repopulated Montana (Mech, 2017). The US Fish and Wildlife Service (USFWS) also successfully reintroduced wolves into Idaho and Wyoming, and individuals from those states moved into Washington, Oregon, and California (Mech, 2017). At this same time reintroduction efforts began in Arizona and New Mexico (Mech, 2017), leaving Colorado one of the few states in the wolves' historic range where they were not regularly present.

Transient wolves have sporadically passed through Colorado since at least the turn of the 21st century, but none had established residency (Colorado Parks & Wildlife, 2022). This changed in 2019 and 2020 when radio-collared wolves from a Wyoming pack were spotted in northwestern Colorado (Colorado Parks & Wildlife, 2022). Additionally, in November 2020 Colorado voters passed a statewide ballot initiative (Proposition 114) that directed Colorado Parks and Wildlife (CPW) to begin reintroduction efforts (Colorado Parks & Wildlife, 2022).

This sequence of events means that beyond simply managing transient wolves that may pass through the state, officials and the public need to plan to live with the wolves as a constant presence.

European settlers arriving in North America saw wolves as threats to human endeavor, pets, livestock, and game animals (Coleman, 2004; Mech, 2017; Niemiec et al., 2022). As wolves return to Colorado today, ranchers, outdoor recreationalists, and members of the public are worried about the presence of wolves near the places they live, work, and play. By early 2022 ranchers in northern Colorado had reported depredation of livestock and working dogs (Blumhardt, 2022a), adding weight to these concerns. Alternatively, conservationists and wolf advocates want to see wolves return to their native range. Conservation groups have successfully fought to have the wolf population in Colorado re-listed on the federal endangered species list (Colorado Parks & Wildlife, 2022; Defenders of Wildlife, n.d.), which limits options for response to human-wolf conflict. As a large carnivore, the presence of wolves in Colorado will require action from the humans who share the state—both those who desire their presence and those who dread it. CPW and USFWS must begin planning now to prevent the escalation of the conflict between wolves and people that will result from both natural expansion and purposeful reintroduction. The use of physical deterrents to mitigate the loss of domestic animals, paired with educational outreach to ranchers, residents, and sportsmen on the appropriate human response to, and realistic threat of, the wolves are crucial to facilitating a successful reintroduction.

Additionally, the wolf population in Colorado will exist under different circumstances than the population from which these wolves migrated. As of April 2022, the wolf population in Colorado is protected under the ESA, which means lethal control is prohibited in the state

(USFWS, 2022). Conversely, the wolf populations in Colorado's nearest wolf-having neighbors—Canada and the Northern Rocky Mountains (including Wyoming, Idaho, and Montana)—are not currently listed under Canada's Canadian Species at Risk Act (Government of Canada, 2017) or the ESA (USFWS, 2022), meaning that tools to address various stakeholder concerns—such as allowing lethal control when wolves threaten livestock— that are utilized in those places are not available in Colorado. However, some lessons for the management of this species, beyond lethal control, can still be learned from actions taken by citizens and organizations in Canada and the Northern Rocky Mountains.

Challenges of Wolf Reintroduction in Colorado

Movement of Wolves into Colorado/ Ballot Measure

After voters passed Proposition 114, but before any formal reintroduction by CPW, a pack of wolves took up residence in northern Colorado, and in 2021 wolf pups were born in the state (Colorado Parks & Wildlife, 2022). At the end of 2020, USFWS delisted gray wolves under the Endangered Species Act (ESA) (USFWS, 2022). Under the direction of Proposition 114, CPW continued to develop a reintroduction plan and was on track to begin wolf reintroduction by the end of 2023 (Colorado Parks & Wildlife, 2022). However, on February 10th, 2022 the species was re-listed federally (USFWS, 2022), which returns authority to the federal government and limits the management actions that can be taken at the state and individual levels. Status under the ESA is often subject to the whims of the political party in power at the federal level—which controls the agencies responsible for listing and delisting, as well as the judicial appointees that hear potential legal challenges to either decision (Bruskotter et al., 2014). This rapid oscillation between state and federal control further complicates management of the tension between wolves and humans in Colorado, as it limits the tools that can be employed and by whom.

Ecological Role of Wolves and Influence on Game Populations

Wolves provide value to an ecosystem as apex predators, regulating ungulate populations and having cascading effects on lower trophic levels (Smith & Peterson, 2021). In Yellowstone, predation by reintroduced wolves directly accounted for 14-18% of elk deaths, though this was less than deaths attributed to black and grizzly bears (Barber-Meyer et al., 2008), and Christianson & Creel (2014) found the wolves were responsible for an overall reduction in elk through both direct and indirect pressures. Reduction in the recruitment of elk calves can be caused indirectly by a "landscape of fear" induced by wolves and similar carnivores in which herbivores spend less time foraging and mating (Halofsky & Ripple, 2008; Laundré et al., 2001). Combined, these effects can dramatically suppress the herbivore population, particularly in ecosystems that have recently lacked a large predator (Christianson & Creel, 2014). While wolves may decrease the herbivore population, this alone is typically not substantial enough to reduce hunting opportunities (Martin et al., 2020). Additionally, the overall effect on the ecosystem can be positive by allowing the recovery of plant species that are over-browsed when herbivore populations get too large (Beschta & Ripple, 2009; Ripple & Beschta, 2012).

Threats to Livestock, Pets, and Humans

In addition to predation of wild herbivores, wolves pose a risk to livestock, pets, and potentially to humans themselves. Wolves account for an average of just over $11,000 worth of livestock losses annually in the northwestern United States (Muhly & Musiani, 2009). While this number, when spread across all farmers and ranchers in the region, represents a small percentage of each operator's income, depredation events are often not equally distributed and a single ranch may bear the brunt of the loss (Blumhardt, 2022a; Muhly & Musiani, 2009). Working dogs on ranches, as well as domestic pets, are also subject to depredation by wolves (Agarwala et al., 2010). Additionally, any large carnivore poses some level of risk to humans, though this direct risk may be low (Olson et al., 2015). Wolf attacks on humans are rare and fairly predictable, with attacks mostly directed at smaller humans and correlated with the presence of pups, which are most vulnerable in late spring (Behdarvand & Kaboli, 2015; Linnell et al., 2003). This means that while the overall risk posed to humans and their livelihoods might be small, it is not negligible for the individuals who will live most closely with the wolves.

Stakeholders

Multiple stakeholders with various values have interests in this conflict. Conservation groups advocate for the presence of wolves, which benefit the overall ecosystem. These same values are shared to some degree by voters in Colorado who passed the ballot resolution to reintroduce wolves. However, ranchers, hunters, and residents of areas where wolves are already moving in, and where they are likely to be reintroduced in the future, are concerned about the potential negative impacts. Ranchers and residents in northwestern Colorado are particularly concerned about the potential for wolves to threaten public safety and livelihoods.

Voters and members of the Public

Voters throughout the state of Colorado approved a statewide ballot initiative that directed CPW to begin efforts to reintroduce wolves to the state (Colorado Parks and Wildlife, 2022). The initiative narrowly passed with voters for and against the wolf reintroduction largely split along urban-rural lines (Ye, 2020; Figure 1). Both sides feel strongly that their vote should carry weight. However, Colorado voters have diverse values based on their potential membership in other stakeholder groups (Niemiec et al., 2020). For example, voters in the urban Denver

Metropolitan Area voted for wolf reintroduction. Urban residents are more likely to share values with conservationists, such as perceiving non-human animals as deserving similar rights and treatment as humans (Manfredo et al., 2021). Their view of the value of wolves to ecosystems may be influenced by the fact that they do not generally live in the part of the state where the wolves will also live (Ditmer et al., 2022). Alternatively, voters from more rural areas—notably those in northwest Colorado where the wolves reside, voted against wolf reintroduction and commonly are members of ranching communities and/or share values with those groups (Ditmer et al., 2022; Manfredo et al., 2021).

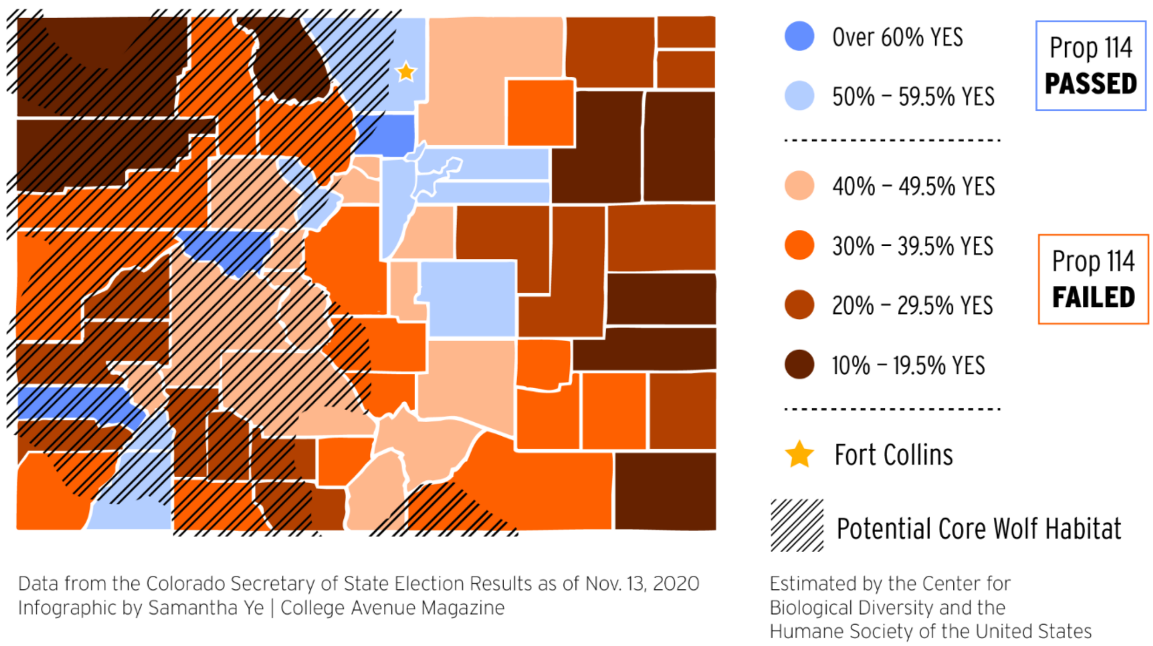

Figure 1 Map of votes for the reintroduction of wolves and probable area for reintroduction. (Ye, 2020)

Hunters

Hunters see the wolves as threatening their ability to hunt elk, deer, and other game that are also prey for wolves (Smith & Peterson, 2021). At the individual level, hunters value the recreation of hunting and for some hunting is the main way they obtain meat to feed their families (Hamilton et al., 2020). These hunters often are knowledgeable about wolves and are concerned that the wolves will make it harder to successfully hunt. Operators of game ranches and outfitters are also concerned about the impact wolves may have on game populations. These stakeholders view wolves as posing a direct threat to herbivores that are often the bread and butter of their operations (Partlow, 2022). These outfitters, and individual hunters, also have concerns about the impact of a general reduction in herbivores—from wolves or other pressures—that results in a corresponding reduction of tags issued (Sakariassen, 2012), limiting the number of people who are able to hunt. The "landscape of fear" induced by wolf presence, leading elk and deer to modify their behavior to more effectively avoid predation from wolves, can also make them more effective at avoiding human predators (Halofsky & Ripple, 2008; Laundré et al., 2001). Therefore, individual hunters and outfitters alike are concerned that the reintroduction of wolves will reduce the presence of the animals they not only value for hunting culturally, but also as their source of meat and income.

Ranchers and Livestock Producers

Ranchers in the area do not want wolves in Colorado. Stockgrowers associations, such as the Colorado Cattlemen's Association which represents and advocates for beef producers in Colorado (Colorado Cattlemen's Association, 2021), voice the concerns of ranchers and livestock producers. Stockgrowers argue that wolves are a threat to livestock and are concerned for the well-being of the animals and the economic consequences of potential losses (Brasch, 2021). Wolves also pose a threat to other animals on ranches, such as working dogs (Swanson, 2022). While compensation programs for damage to property (including livestock and working dogs) from predators do exist, there are often challenges such as long wait times, requirements of prevention efforts, and the burden of proving the culprit of an attack (Brasch, 2021; Colorado Parks and Wildlife, 2020). This hurdle, paired with the increase in the price of land and other requirements for cattle production in recent years compounds the toll wolves take on these operations (Muhly & Musiani, 2009). These factors contribute to the ranchers' concern that wolf presence could have negative ramifications for the production of their cattle, and compound with other challenges to have broader impacts on their livelihoods and way of life.

Conservationists and Wolf Advocates

Conservationists and wolf advocates are interested in seeing the wolves restored in Colorado because it represents part of their historic range. The organization Defenders of Wildlife in particular has advocated for the presence and protection of wolves in Colorado (Defenders of Wildlife, n.d.). Conservationists often cite ethical support for wolves to return to land on which they existed in the past, particularly as a part of the conservation of the species (Niemiec et al., 2020). They also value the ecological benefit of having apex predators controlling a trophic cascade (Niemiec et al., 2020). These values drive conservationists—both individuals and conservation-focused organizations—to advocate for the presence of wolves in suitable habitat, even if that habitat is far from where they themselves live (Ditmer et al., 2022).

Recommendations

By coordinating with stakeholders in advance of escalating conflict, CPW and USFWS can enact a plan to mitigate the negative consequences of the wolves in the parts of the state where they reside and meet the needs of both wolves and humans. This plan should rely on previous experiences with wolf reintroduction in North America and around the world. The recommendations contained here assume federal control of the species, given the listing of wolves under the ESA, but could be adapted if the federal status changes and CPW becomes the sole administrator. USFWS should classify the wolf population in Colorado as a "non-essential experimental population" under section 10 (j) of the ESA (Fitzgerald, 2018) to ease this likely transition between federal and state control. The designation of the population as "non-essential" eases the restrictions on dealing with the wolves and makes things like lethal management legal in some circumstances. Manzolillo (2021) found that the option of lethal control in parts of the country such as Montana and Wyoming where wolves have already been reintroduced made landowners feel they had greater control over the situation, and improved overall feelings about the presence of wolves, highlighting the importance of this tool for successful reintroduction.

A core part of the successful management of wolf-human interactions as both species expand in Colorado involves federal agencies and stockgrowers partnering with conservation organizations. Partnerships between conservation organizations and ranchers and other stakeholders have been vital to the successful co-existence between wolves and people in Idaho, Montana, and Wyoming (Manzolillo, 2021). Such collaboration should be used for programs such as recruiting volunteer range riders. Range riders patrol properties including farms, cattle ranches, and game ranches where land managers are concerned about wolf depredation. This strategy has been somewhat successful already in Colorado, where a wolf advocate volunteered to patrol a ranch that had seen livestock depredation (Blumhardt, 2022b). Range riders have been successful in the Northern Rockies as well because they are on the ground directly responding to wolf presence, and because ranch operators are receptive to the possibility of hiring someone from within the community (Manzolillo, 2021). Recruiting people for this work, who are likely to value the presence of wolves (Blumhardt, 2022b), could be a key application of the reach of conservation organizations.

Other non-lethal deterrents should also be used. Electric fences, bright lights, and noisemakers are already deployed in the rest of the country (Richard, 2022) and effectively startle wolves so they do not become habituated to the easy prey of domestic cattle (Gese et al., 2021). Dogs and burros are also options for deterring wolves from livestock (Kirk, 2022; Musiani & Paquet, 2004), and Gehring et al. (2010) found dogs, in particular, were effective at preventing depredation by wolves in the upper midwest. Programs to assist landowners with these investments already exist in Colorado (Blumhardt, 2022b; Colorado Parks and Wildlife, 2020), but this is another place where conservation organizations that are keen to see the success of the wolves' reintroduction could partner to raise funds.

Part of effective deterrence will involve education and outreach by conservation organizations such as Defenders of Wildlife and government agencies, particularly CPW, to ranchers, residents, and hunters to dispel misinformation about wolves. The first step is to educate concerned parties about the realistic threats posed by wolves to humans, their livestock, pets, and big game, as well as benefits to the overall ecosystem and how this may serve their interests. Education of humans in the area would mean attention could be diverted away from things of lesser concern, such as direct attacks on humans, and towards hazing and other activities that would deter wolves from their property.

In addition, because these tools may take time to implement, and effectiveness in each situation may vary, compensation for depredation of livestock should be readily dispensed in cases where wolf activity is likely. Most compensation programs throughout the US and Canada where wolves already reside require an agency representative assessing the kill to conclusively find that a wolf was responsible, and then pay out only the market value of the animal (Muhly & Musiani, 2009). This is insufficient to resolve the conflict because depredation by wolves is not provable every time and compensation for the animal alone likely does not represent the full cost to the operator of that loss (Manzolillo, 2021; Muhly & Musiani, 2009). The addition of a "pay for presence" type program that has been employed in other places such as Sweden (Musiani & Paquet, 2004) and the Southwestern US (Manzolillo, 2021) may be beneficial. In the northwestern US conservation organizations such as Defenders of Wildlife also raise money to support more robust compensation (Manzolillo, 2021), indicating another place where a partnership between the conservationists in favor of the wolves and the dubious ranchers would benefit all parties.

Conclusion

While the issue of wolves returning to Colorado is poised to be rife with strife, there are a few simple steps that can foster co-existence between humans and this wild canid. The predominant strategy to manage this conflict is for CPW and USFWS to collaborate with stakeholders to plan in advance, leveraging lessons from around the world, for dealing with sources of tension. Successfully navigating wolf reintroduction in Colorado will require that groups with apparently contradictory values—namely conservationists and ranchers— work together, rather than in opposition, to protect both the wolves and human livelihoods.

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