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By

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Committee in charge:

Professor Arthur D. Middleton, Chair
Professor Justin S. Brashares
Professor Christopher J. Schell

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Abstract

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To combat declines in biodiversity, conservationists are increasingly looking to restore wildlife populations through the reintroduction of select species, the establishment of protected areas, and the use of human-wildlife conflict mitigation tools. A primary objective of wildlife restoration efforts is to reestablish trophic interactions crucial for the function and structure of ecosystems. However, recovering wildlife populations are often returning to novel ecosystems with altered environments and new species compositions. These novel ecosystems may then complicate the outcomes of wildlife restoration efforts. In Chapter 1, I provide a brief introduction to key themes of wildlife restoration in novel ecosystems. In Chapter 2, I evaluate the outcomes of wildlife translocations around the world. Specifically, I evaluate whether the inclusion of human dimensions in the planning and execution of a translocation improves success. Next, for my final two chapters, I zoom in to Argentine Patagonia to better understand how a novel environment impacts the outcomes of wildlife restoration. In Chapter 3, I assess how roads influence the habitat selection of the most widespread large herbivore in Patagonia, the guanaco. In addition to the creation of novel landscapes, habitat restoration in the region has led to a novel interaction between pumas and penguins. In Chapter 4, I test how this novel interaction between pumas and penguins impacts puma behavior and their population. Then building on these results, for Chapter 5, I examine the impacts of the puma-penguin interaction on guanacos, the primary prey for guanacos throughout Patagonia. Finally in Chapter 6, I close with some concluding remarks about wildlife restoration in novel ecosystems.

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Chapter 1. Introduction

The rapid decline of biodiversity worldwide stands as one of humanity's greatest existential threats. In just this past century, over 200 vertebrate species have gone extinct, with many more facing significant population declines (Ceballos et al., 2017). This accelerating loss of biodiversity alters ecological webs, jeopardizes food security, erodes cultural connections to nature, disrupts natural disease control mechanisms, and diminishes the ability of ecosystems to adapt to climate change (Ceballos et al., 2015, 2017; Dirzo et al., 2014; Young et al., 2016). Despite these challenges, conservationists have made notable progress (Aronson et al., 2020; Chapron et al., 2014; Loch et al., 2020). Through the establishment of protected areas, targeted reintroductions, human-wildlife conflict reduction programs, and the development of wildlife corridors, some species are beginning to make significant recoveries (Maxwell et al., 2020; Mimet et al., 2016; Nyhus, 2016; Watson et al., 2014). The critical urgency of restoring biodiversity is underscored by a growing wave of conservation initiatives and international agreements targeting the restoration of wildlife and their habitat including the United Nations Decade on Restoration, 30x30, and the Kunming-Montreal Global Biodiversity Framework (Aronson et al., 2020; Dinerstein et al., 2019; Tsioumani, 2020).

Given the urgency of effective conservation action, rigorously evaluating conservation outcomes to determine when, where, and how these measures are most effective has become a global priority (Cazalis et al., 2020; Gatiso et al., 2022; Geldmann et al., 2013, 2015, 2021). This is particularly important as the success of many conservation strategies have provided, at best, mixed results (Bellis et al., 2020; Berger-Tal et al., 2020; Coad et al., 2019; Maxwell et al., 2020). For example, while the coverage of protected areas has grown considerably over the last few decades, the biodiversity within them continues to decline (Maxwell et al., 2020). Several ecological, social, and political factors may contribute to the limited effectiveness of conservation measures, including insufficient resources, lack of institutional support, difficulty in securing community buy-in, and the inability to abate other threats to biodiversity (e.g. invasive species) (Berger-Tal et al., 2020; Coad et al., 2019; Geldmann et al., 2015; Maxwell et al., 2020). Therefore, analyses to understand the determinants of success for various conservation measures are important for improving their outcomes.

Wildlife translocations, or the intentional movement of organisms from one site to another for the benefit of conservation, is increasingly used as a tool to reintroduce and reinforce wildlife populations (Serota, 2024). However, like other conservation strategies, wildlife translocation efforts have been met with mixed results (Batson et al., 2015; Bellis et al., 2020; Berger-Tal et al., 2020). To understand what makes wildlife translocation successful, researchers have traditionally investigated ecological or programmatic factors like climate suitability, habitat quality at the release site, origin of the source population, and the number of animals reintroduced (Batson et al., 2015; Bellis et al., 2020; Berger-Tal et al., 2020; Bubac et al., 2019; Morris et al., 2021). However, as the focus of conservation shifts towards shared human-wildlife landscapes, the success of translocations hinges on our ability to foster coexistence (Carter & Linnell, 2016). Thus, human dimensions, or the social, political, psychological, economic, and cultural components of conservation, are increasingly recognized as critical to the success of conservation (Bennett et al., 2017; Niemiec et al., 2021). In Chapter 2, I evaluate the prevalence of incorporating human dimensions in wildlife translocations and whether their inclusion impacts success. To identify relationships between the inclusion of human dimension objectives in wildlife translocation efforts and program outcomes, we synthesized information from case studies reported in the International Union for Conservation of Nature (IUCN) Global Re-Introduction Perspective Series (Soorae, 2008, 2010, 2011, 2013, 2016, 2018, 2021). We tested whether the inclusion of human dimensions increased the probability of a positive outcome and the primary factors determining whether case studies even included human dimensions.

Assessing the effectiveness of some conservation measures is straightforward, such as survival and reproduction of translocated species. However, evaluating the restoration of multispecies dynamics like trophic interactions and their resulting ecological effects (e.g. trophic cascades) can be challenging (Tylianakis et al., 2010). Evaluating these critical outcomes of wildlife restoration becomes even more challenging when restoration efforts occur amid significant ecological change. Since some species were originally extirpated decades ago, anthropogenic change has reshaped our environment leading to novel ecosystems (Hobbs et al., 2009; Radeloff et al., 2015). A novel ecosystem is a measurable dissimilarity between the baseline and current ecological conditions; thus, all ecosystems have some degree of novelty, though the extent of novelty may vary (Radeloff et al. 2015). The incidence of novel ecosystems and their magnitude are growing as global trade facilitates the spread of invasive species, human development creates novel habitats and shifts species distributions, and a changing climate creates novel abiotic conditions (Radeloff et al., 2015). The outcomes and effectiveness of conservation in novel ecosystems can be difficult to assess as they can lead to new species behaviors, interspecific dynamics, and ecosystem processes.

A primary objective of wildlife restoration is to reestablish key trophic interactions–like herbivory, seed dispersal, and predation–that shape ecosystems (Loch et al., 2020; Perino et al., 2019). However, novel ecosystems can complicate these relationships. Novel ecosystems can reshape the resource landscape for wildlife impacting when, where, and how animals obtain food, seek shelter, and acquire mates (Guiden et al., 2019; Valentine et al., 2020). For example, Manatees (*Trichechus manatus*) in Florida aggregate at warm-water discharges from power plants during the winter, while white storks (*Ciconia ciconia*) use electricity pylons as nesting sites in Portugal (Laist & Reynolds III, 2005; Valentine et al., 2020). How animals respond to changing resource dynamics in novel ecosystems not only impacts their own survival and individual fitness, but it can also shape population dynamics, species interactions, and the transport of nutrients across landscapes.

The Patagonian Steppe was once inhabited by an abundance of large herbivores including guanacos (*Lama guanicoe*), and their predator, the puma (*Puma concolor*) (Walker & Novaro, 2010). Over the last 10,000 years, the pumas-guanaco predator-prey interaction was the sole large predator, large prey interaction in the steppe (Donadio, Zanón

Martínez, et al., 2022). However, following European colonization of Argentina, herbivore numbers declined in the region due to conflict with livestock production; domestic sheep replaced guanacos across much of the steppe (Walker & Novaro, 2010). In addition, predators like the puma were extensively hunted to protect livestock. The loss of mainland predators like the puma is hypothesized to have triggered the rapid expansion of Magellanic penguin (*Spheniscus magellanicus*) colonies and their population across the coast of Argentina (Borboroglu & Boersma, 2013; Cruz et al., 2014). Prior to European colonization, Magellanic penguins are largely thought to have been restricted to offshore islands without terrestrial predators (Borboroglu & Boersma, 2013; Cruz et al., 2014).

Argentina is an emerging leader in wildlife restoration (Donadio, Di Martino, et al., 2022; Donadio, Zamboni, et al., 2022). In the Patagonian steppe of Argentina, collaboration between the Tompkins Foundation and the Argentine government has led to the protection of more than 14 million acres of land (Pereira et al., 2020; Zorondo-Rodríguez et al., 2019). These efforts have led to local recoveries of both guanaco and puma populations (Barri, 2016; Walker & Novaro, 2010). However, since the decline of pumas and guanacos in the early 20th century, Patagonia has dramatically changed. Both pumas and guanacos are now recovering in ecosystems that have been significantly altered since they were originally extirpated; they now find themselves in novel landscapes (e.g. highways and resource extraction activities like mining and oil exploration) with novel species compositions (e.g. Magellanic penguins and European hares, *Lepus europaeus*). However, it's unclear how this novel ecosystem affects the outcomes for recovering pumas and guanacos, including their behaviors, populations, and predator-prey relationship.

In Chapter 3, I explore the effects of a novel landscape (highways) on guanaco behavior. Roads are among the most widespread habitat modifications on the planet (Meijer et al., 2018). However, there is considerable variation in how animals respond to roads, which can vary both across and within species (Hill et al., 2021; Teixeira et al., 2020). Additionally, certain behaviors (e.g. resting or foraging) may impact whether individuals are attracted to or repulsed by roads (Abrahms et al., 2016). In this chapter, I integrate multiple movement analyses to test how different behaviors (resting, foraging, or traveling) impact 1) whether guanacos select for or against proximity to roads, and 2) whether guanacos select for or against crossing them.

Next, in Chapter 4, I evaluate how a novel resource (penguins) impacts puma behavior and population dynamics. Monte León National Park (MNLP), a protected area established during the current surge in conservation interest along Argentina's coast, is home to a large breeding colony of Magellanic penguins. Shortly after the park was established in 2004, penguin remains were found in puma scat for the first time ever (Zanón Martínez et al., 2012). However, we know very little about this interaction beyond the existence of puma predation of penguins. Thus, Chapter 4 tests how puma predation of penguins impacts both puma behavior and population dynamics at MNLP.

Lastly, in Chapter 5 I examine how this novel resource (penguins) impacts the predator-prey relationship between pumas and guanacos. Novel ecosystems can shift the distribution of resources, thereby impacting foraging strategies for predators (Guiden et al., 2019; Valentine et al., 2020). In multi-prey systems, if predators prefer one prey type over another, they may need to shift their habitat use to better exploit that prey type. This change in foraging behavior and habitat use may then impact where prey experience risk on the landscape. For Chapter 5, we test how the risk of predation for primary prey (guanacos) is altered by a seasonally-abundant novel alternative prey (penguins).

Chapter 2. Incorporating Human Dimensions is Associated with Better Wildlife Translocation Outcomes

This chapter has been previously published and is included here with permission from co-authors.

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ABSTRACT

Wildlife translocations are increasingly used to combat declining biodiversity worldwide. Successful translocation often hinges on coexistence between humans and wildlife, yet not all translocation efforts explicitly include human dimensions (e.g., economic incentives, education programs, and conflict reduction assistance). To evaluate the prevalence and associated outcomes of including human dimensions as objectives when planning translocations, we analyze 305 case studies from the IUCN's Global Re-Introduction Perspectives Series. We find that fewer than half of all projects included human dimension objectives (42%), but that projects including human dimension objectives were associated with improved wildlife population outcomes (i.e., higher probability of survival, reproduction, or population growth). Translocation efforts were more likely to include human dimension objectives if they involved mammals, species with a history of local human conflict, and local stakeholders. Our findings underscore the importance of incorporating objectives related to human dimensions in translocation planning efforts to improve conservation success.

INTRODUCTION

Over the last century, more than 200 vertebrate species have gone extinct, and many more have experienced range contractions, extirpations, and population declines(Ceballos et al., 2017). Wildlife translocation, defined here as the intentional movement of organisms from one site to another for the benefit of conservation serves as an increasingly important tool to combat widespread declines in global biodiversity (Bubac et al., 2019; Crees et al., 2016; Jachowski, David S.; Millspaugh, Joshua, J.; Angermeier, Paul, L.; Slotow, 2016; Seddon et al., 2007). However, wildlife translocation programs have been met with mixed results. High-profile wildlife translocation success stories include the reintroduction of Arabian oryx (*Oryx leucoryx*) throughout the Arabian Peninsula and the peregrine falcon (*Falco peregrinus*) throughout the United States (Bruggeman et al., 2015; Mizera & Sielicki, 2009; Spalton et al., 1999). Conversely, reintroduced populations of brush-tailed bettongs (*Bettongia penicilliata*) in Australia and red wolves (*Canis rufus*) in the United States swiftly declined to unsustainable levels (Priddel & Wheeler, 2004; U.S. Fish & Wildlife Service, 2021). Translocation programs require considerable time and resources, and their failure can lead to distrust between stakeholders, the loss of resources, and even the extinction or extirpation of entire populations or species (Hilbers et al., 2020; Jachowski, David S.; Millspaugh, Joshua, J.; Angermeier, Paul, L.; Slotow, 2016). Thus, understanding why some efforts succeed where others fail is key to designing future wildlife translocation programs and allocating scarce conservation resources. To date, such understanding has remained elusive, likely due in part to the underreporting of conservation struggles relative to successes (Catalano et al., 2019; Godet & Devictor, 2018).

Investigations into common drivers of wildlife translocation success have largely focused on biological and ecological factors such as climate suitability, reintroduction site quality, source population origin, and the number of reintroduced individuals (Bellis et al., 2020; Bubac et al., 2019; Fischer & Lindenmayer, 2000; Morris et al., 2021). However, as conservation efforts increasingly occur in landscapes shared by humans and wildlife, the success of translocations has become more reliant on coexistence with people (Carter & Linnell, 2016). Therefore, human dimensions, or the social, political, psychological, economic, and cultural components of conservation, are increasingly recognized as critical to the success of wildlife translocations (Bennett et al., 2017; Bruskotter & Wilson, 2014; Niemiec et al., 2021; Schultz, 2011). Human dimension-related activities in wildlife conservation can be either foundational (providing information needed to understand the local context and stakeholders) or functional (being directly applied to management issues) (Sexton et al., 2013).

Incorporating human dimensions may ultimately prove as important to achieving conservation goals – if not more important - than biological or environmental factors, because most threats to wildlife are directly attributed to humans (Mascia et al., 2003). Indeed, human dimensions have informed the design of translocations across multiple taxa including fish (Christie et al., 2017), mammals (Esmaeili et al., 2019; Titus & Jachowski, 2021), birds (Dayer et al., 2020; Psuty & Całkiewicz, 2021), reptiles (Ashley et al., 2007), and amphibians (Hartel et al., 2020; Karlsdóttir et al., 2021). Examples include resource provisioning to protect livestock from translocated wildlife, education programs in local communities and schools, media campaigns to influence attitudes towards wildlife, economic benefits for landowners living with wildlife, and legal enforcement against illegal wildlife trade. Many groups working to reintroduce wildlife now integrate social and ecological information into their conservation plans to better predict areas of wildlife tolerance, potential conflicts, and the distribution of benefits to local communities (André et al., 2022; Ditmer et al., 2022; McCann et al., 2021; Smith et al., 2008). In the IUCN Guidelines for Reintroductions and Other Translocations, the inclusion of human dimensions is considered integral to the design, implementation, and evaluation of translocations (IUCN/SSC, 2013). However, despite the recognized importance of human dimensions, these factors are still largely missing from many conservation initiatives (Fox et al., 2006; Niemiec et al., 2021; Welch-Devine & Campbell, 2010). Potential explanations for this gap includes scarcity of resources, administrative and funding legacies, and lack of interdisciplinary collaborations (Fox et al., 2006). Although many individual case studies highlight the importance of including human dimensions in the design and implementation of wildlife translocation programs, overarching relationships between translocation success and human dimension considerations have not been comprehensively evaluated.

To identify relationships between the inclusion of human dimension objectives in wildlife translocation efforts and program outcomes, we synthesized information from case studies reported in the International Union for Conservation of Nature (IUCN) Global Re-Introduction Perspective Series (Soorae, 2008, 2010, 2011, 2013, 2016, 2018, 2021). First, we tested whether setting human dimension objectives increased the probability of a positive outcome (i.e., widespread survival, reproduction, or population growth) for the translocated wildlife population. Second, we identified the primary factors influencing whether translocation efforts set human dimension objectives. We predicted that the probability of including human dimensions in project objectives would be higher (a) for projects translocating wider ranging taxa like mammals and birds whose broad ranges often overlap with human-influenced areas, (b) in areas where the key threats to the species were locally attributed to humans, (c) where humans have experienced conflict with the species of interest, and (d) when local stakeholders played an active role in the project (Table S1). Additionally, given increasing attention to human dimensions in conservation and their explicit recommendation in the IUCN Guidelines for Reintroductions and Other Translocations published in 2013, we predicted that the inclusion of human dimension objectives would increase over time.

We found evidence that explicitly setting objectives related to human dimensions was associated with an increased probability of a positive outcome for the translocated wildlife population. However, fewer than half of all case studies included human dimension objectives when planning their translocation. Translocation efforts conducted without including local community members, for example those led solely by academic institutions, governments, non-profits, or zoos, were less likely to have a positive outcome. The probability of setting human dimension objectives was higher for restoration efforts of mammals and birds and for species with local threats directly related to humans or a reported history of human-wildlife conflict. Promisingly, the inclusion of human dimension objectives in wildlife translocations has increased over time. Our results underscore the importance of human dimensions in wildlife translocation success, revealing that translocations and conservation efforts benefit from incorporating human-related factors along with biological and environmental considerations.

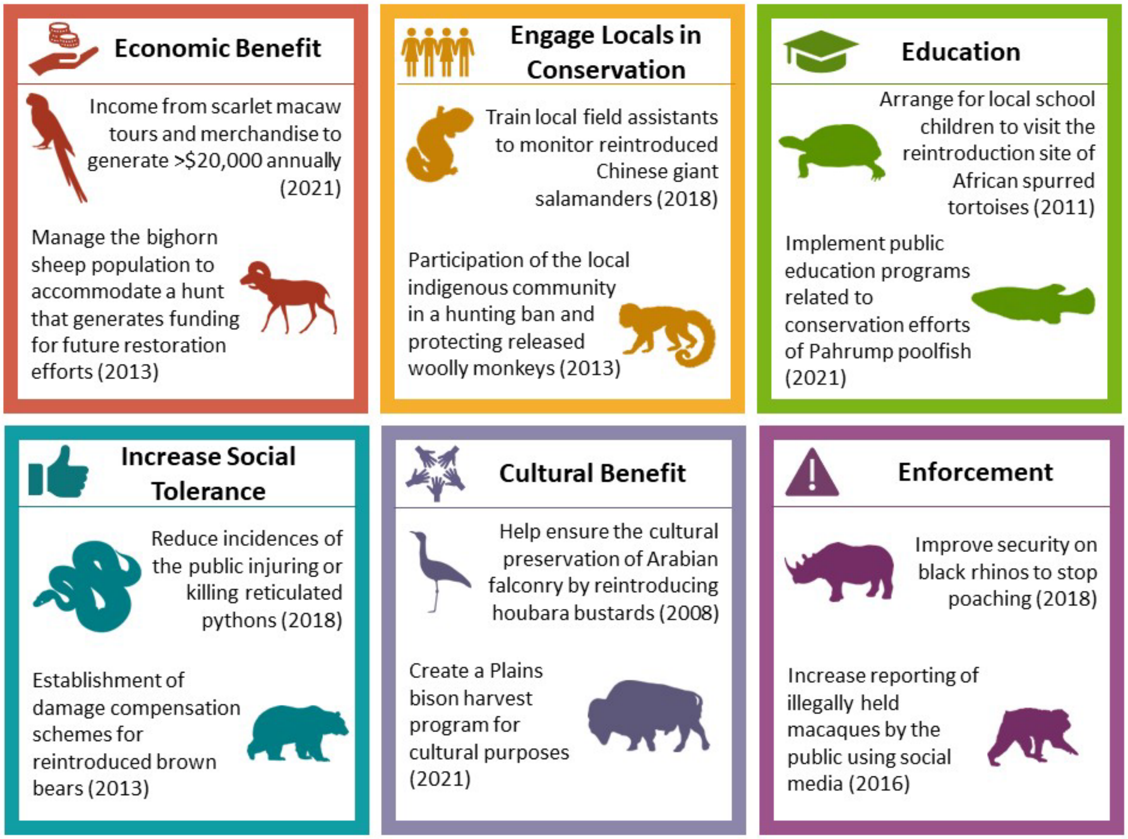
METHODS

IUCN Global Re-introduction Perspectives Series

The IUCN Global Re-introduction Perspectives Series publishes conservation translocation case studies of plants, invertebrates, amphibians, reptiles, birds, fish, and mammals from around the world (Soorae, 2008, 2010, 2011, 2013, 2016, 2018, 2021). The goal of the series is to provide a global synthesis of the challenges facing biodiversity translocation projects. The series has published 7 volumes from 2008 - 2021. All case studies share the same structure with the following sections: Introduction, Goals, Success Indicators, Project Summary, Major Difficulties Faced, Major Lessons Learned, and a self-evaluated ranking of the success of the project with a section on the Reason(s) for Success. Participants in the series are given a blank template and a few examples of case studies from previous volumes to draw upon. The format provides a standardization not otherwise possible with traditional literature reviews. However, the abbreviated format and self-reporting nature likely does not encompass every detail of the translocation, nor does the collection of case studies chronicle every wildlife translocation attempt. For this analysis, we focused on case studies of all vertebrates (n = 305). In total, there were 268 unique species in the dataset.

Data Collection and Categorization

For each case study, we evaluated whether each section in the report (Goals, Success Indicators, Major Difficulties Faced, and Major Lessons Learned) contained information related to the human dimensions of the translocation. We defined setting human dimension objectives as a binary yes/no based on whether the project explicitly included either a Goal or Success Indicator that related to any aspect of human-related cultural, political, economic, social, or psychological considerations (Riley & Sandström, 2013). We then identified six key strategies into which we categorized each human dimension related Goal or Success Indicator: providing education, engaging locals, increasing social tolerance, supplying economic benefits, enforcing regulations, and improving cultural benefits (Fig. 1). In addition, we recorded the location, start year of the project, groups or stakeholders involved in the translocation, threats to the species, and whether there was a history of conflict reported between that species and humans in the translocation area. The group(s) or stakeholder(s) for each translocation were identified from the authors' affiliations and the Project Summary of each case study and were classified as government, academic, zoo, non-profit, local community, private landowner, and private company. Stakeholder classifications were based on project involvement; therefore, many case studies included multiple groups. The threats to each species were classified according to the IUCN Red List of Threatened Species Database and included direct human threats (e.g., residential & commercial development, agriculture & aquaculture, energy production & mining, transportation & service corridors, biological resource use, human intrusion & disturbance, natural systems modification), and indirect human threats (e.g., invasive & other problematic species, genes & diseases, pollution, and climate change & severe weather) (IUCN, 2022).



Economic Benefit

Income from scarlet macaw tours and merchandise to generate >$20,000 annually (2021)

Manage the bighorn sheep population to accommodate a hunt that generates funding for future restoration efforts (2013)

Engage Locals in Conservation

Train local field assistants to monitor reintroduced Chinese giant salamanders (2018)

Participation of the local indigenous community in a hunting ban and protecting released woolly monkeys (2013)

Education

Arrange for local school children to visit the reintroduction site of African spurred tortoises (2011)

Implement public education programs related to conservation efforts of Pahrump poolfish (2021)

Increase Social Tolerance

Reduce incidences of the public injuring or killing reticulated pythons (2018)

Establishment of damage compensation schemes for reintroduced brown bears (2013)

Cultural Benefit

Help ensure the cultural preservation of Arabian falconry by reintroducing houbara bustards (2008)

Create a Plains bison harvest program for cultural purposes (2021)

Enforcement

Improve security on black rhinos to stop poaching (2018)

Increase reporting of illegally held macaques by the public using social media (2016)

Fig. 1: Strategies used to incorporate human dimensions in wildlife translocation. Strategies were identified based on human dimensions reported in project goals or success indicators from case studies in the IUCN Global Re-Introduction Perspective Series; the figure includes key examples from each strategy (Soorae, 2008, 2011, 2013, 2016, 2018, 2021)

The success of wildlife translocations can be measured in multiple ways including changes to the target population, impacts to the ecosystem, and knowledge gained from the project. In the IUCN Global Re-introduction Perspectives Series, all authors rate the success of the project from ‘Highly Successful’ to ‘Failure.’ However, there may be inconsistency in how the authors of different projects define success. Therefore, we classified the outcome of the project as positive or negative based on the outcome to the wildlife population reported in the Project Summary and Reason(s) for Success sections of the reports. Case studies that we classified as having a positive outcome reported on a scale of widespread survival, reproduction, and/or population growth, whereas case studies classified as a negative outcome reported either widespread mortality or population extinction (Table S2). Therefore, case studies only needed to report a minimum of widespread survival of the translocated individuals to be classified as a success. We used a binary positive or negative outcome instead of each individual outcome to reduce bias from the species in the case study (e.g., differences in generation times) or project (e.g., length of project) which could greatly impact differences in the reported outcome (e.g., survival vs. reproduction). Further, the binary outcome also increased the repeatability in our assessment of the project due to the clear differences between positive (widespread survival, reproduction, or population growth) and negative (widespread mortality and population extinction) outcomes.

We classified human dimension objectives and wildlife population outcomes through a collaborative calibration process. First, each coauthor independently evaluated thirty case studies to identify broad classifications of human dimension strategies. Next, we worked together to synthesize and refine classifications to comprehensively cover all human dimensions reported. We then reviewed all projects using the classification framework ensuring consistency by discussing all potentially ambiguous classifications with the entire group.

Analysis of Human Dimension Objectives Across Wildlife Translocations

We used a series of logistic regression models to test our predictions related to human dimensions. First, we assessed whether the inclusion of human dimension objectives affected the outcomes of wildlife translocations using a multivariate logistic regression model with the translocation outcome (positive or negative) as the response variable and whether the project included human dimension objectives as a binary predictor variable. We also included two factors that may impact the reported outcomes as a predictor variable: 1) project time length, because longer project time lengths could increase the probability of observing a positive outcome, and 2) taxa, since population increases could be more difficult to identify in taxa with longer generational times.

Next, we examined how the inclusion of human dimension objectives (as a binary response) varied among taxonomic groups, threats to the species, existence of a local history of conflict with the species, and the stakeholder groups involved in the translocation. We evaluated differences for each variable using Tukey's post-hoc pairwise comparisons. To compare the relative importance of each variable, we then conducted a multivariate logistic regression with the inclusion of human dimension objectives as the binary response and the taxonomic group, existence of a local history of conflict with the species, whether the translocation involved local community groups, and whether one of the listed IUCN threats was a direct human threat as covariates.

Finally, to evaluate changes in the inclusion of human dimension objectives over time, we used two separate univariate logistic regressions with the inclusion of human dimension objectives as a binary response variable. One model included the restoration start year as the predictor variable; the other included a binary variable representing whether the case studies occurred before or after 2014 to capture whether the inclusion of objectives related to human dimensions increased following the publication of the IUCN Guidelines for Reintroductions and Other Conservation Translocations in 2013. All statistical analyses were conducted in R version 4.0.2, and we defined statistical significance based on an alpha level of 0.05 (R Core Team, 2021). We generated figures using the 'ggplot2' package in R (Wickman, 2016).

RESULTS

We analyzed 305 case studies of wildlife translocations from 7 IUCN reports published between 2008 and 2021. Translocations occurred from 1922 to 2018 and included 121 mammals, 77 birds, 40 fish, 40 reptiles, and 27 amphibians. Most case studies occurred in North America (n = 69) and Asia (n = 67), followed by Oceania (n =56), Europe (n = 53), Africa (n = 35), and South America (n = 25). Of the 305 case studies, 127 case studies (42%) included human dimension objectives in either their Goals or Success Indicators. One hundred and seventy-three case studies (57%) included human dimensions in either their Lessons Learned or Major Difficulties Faced, 76 of which (43%) did not include human dimension objectives in their Goals or Success Indicators. Most projects resulted in a positive outcome (n = 272); approximately 11% (n = 33) reported a negative outcome. Overall, translocation efforts that included human dimension objectives were significantly more likely to have a positive outcome (0.94; 95% CI=0.88-0.97) than the translocation efforts that did not include human dimension objectives (1.02, 95% CI=0.07-2.10; $p < 0.01$). Both project time length and taxa were insignificant ($p > 0.05$ in both cases).

Of the six key strategies we identified for including human dimension objectives, education was the most common (n = 111), followed by engaging locals (n = 96), providing economic benefits (n = 41), increasing social tolerance (n = 32), enforcing regulations (n = 19), and supplying cultural benefits (n = 9).The inclusion of human dimension objectives varied significantly between taxonomic groups, threats to the species, the groups involved in the restoration, and whether the authors reported a history of human conflict. Across taxonomic groups, translocation efforts of both mammals (0.53; 95% CI=0.44 - 0.62) and birds (0.41; 95% CI=0.31-0.53) had a significantly higher probability of including human dimension objectives than amphibians (0.15; 95% CI=0.06-0.34) ($p < 0.01$ and $p = 0.01$, respectively; Fig. 2). Translocation efforts of mammals also had a higher predicted probability of including human dimension objectives compared to fish (0.33; 95% CI=0.20=0.48; $p = 0.02$; Table S3). Case studies that reported a history of conflict with the species had a predicted probability of including human dimension objectives of 0.62 (95% CI=0.50-0.73), significantly higher than the predicted probability of including human dimension objectives for translocation efforts of a species without a history of conflict of 0.36 (95% CI=0.30-0.42; $p < 0.01$).

Translocation efforts that involved local communities (0.63; 95% CI=0.50- 0.73) and private landowners (0.68; 95% CI=0.53-0.80) were significantly more likely to include human dimension objectives than restoration efforts that involved academics (0.39; 95% CI=0.32-0.48), zoos (0.35; 95% CI=0.26-0.46), government agencies (0.42; 95% CI=0.36-0.49), nonprofits (0.47; 95% CI=0.39-0.54), and private companies (0.50; 95% CI=0.31-0.69) ($p < 0.05$ in all cases, Fig. 3, Table S4). Translocation efforts that involved local communities had a significantly higher predicted probability of a positive outcome (0.97, 95% CI=0.88-0.99) than translocation efforts that involved academics, non-profits (0.87; 95% CI=0.81-0,91), and private companies (0.83; 95% CI=0.63-0,93). Finally, case studies where the species was threatened by transportation and service corridors, energy production or mining, agriculture or aquaculture, and biological resource use had the highest predicted probability of including human dimension objectives, whereas translocation efforts where the species was threatened by climate change, invasive species, and natural system modifications had the lowest predicted probability of including human dimension objectives (Table S4).

After we identified taxonomic groups, stakeholder groups involved in the translocation, IUCN threats, and a local history of conflict as significant predictors of the inclusion of human dimension objectives, we evaluated the relative importance of each predictor in a global model. Like the univariate model results, whether the species was a mammal, local history of conflict, and whether the translocation involved local community groups were all significant predictors of including human dimension related objectives (Table S6). However, the translocation of fish taxa and the presence of a direct human threat were no longer significant when considered in conjunction with the other variables ($p > 0.05$ in both cases; Table S6).

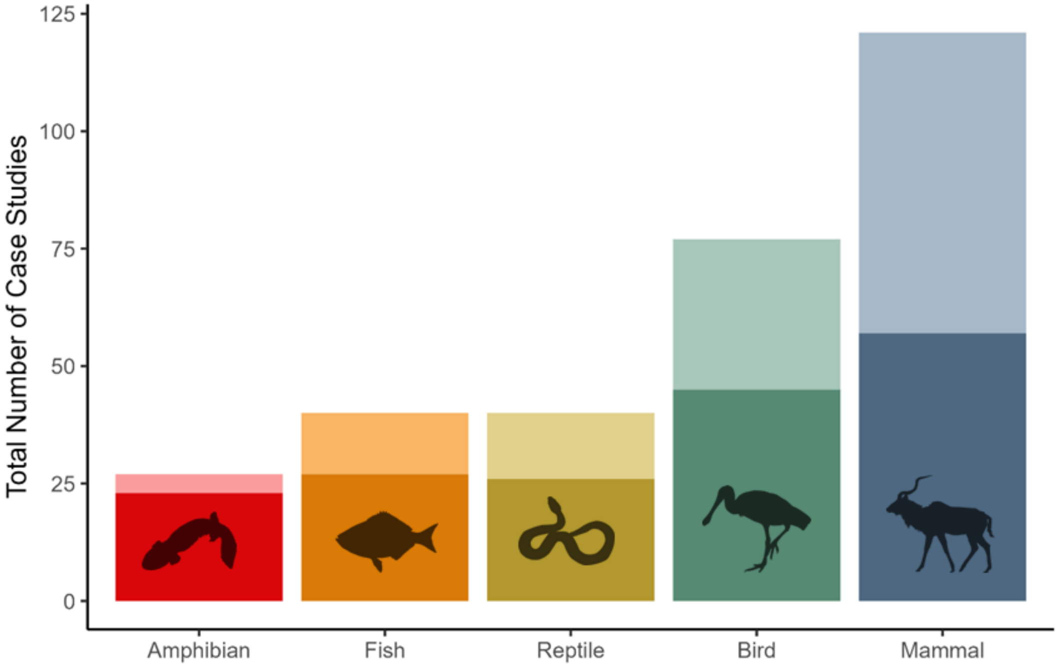


Fig 2. Inclusion of human dimension objectives in wildlife translocations varied among taxa. Data is based on case studies from the IUCN Global Re-introduction Perspectives Series (2008-2021). Lighter shading indicates the number of case studies that included human dimension objectives; darker shading represents case studies that did not include human dimension objectives. By taxon, the percent of translocations that did not include human dimension objectives were: Amphibians: 85%; Fish: 68%; Reptiles: 65%; Birds: 58%; Mammals: 47%.

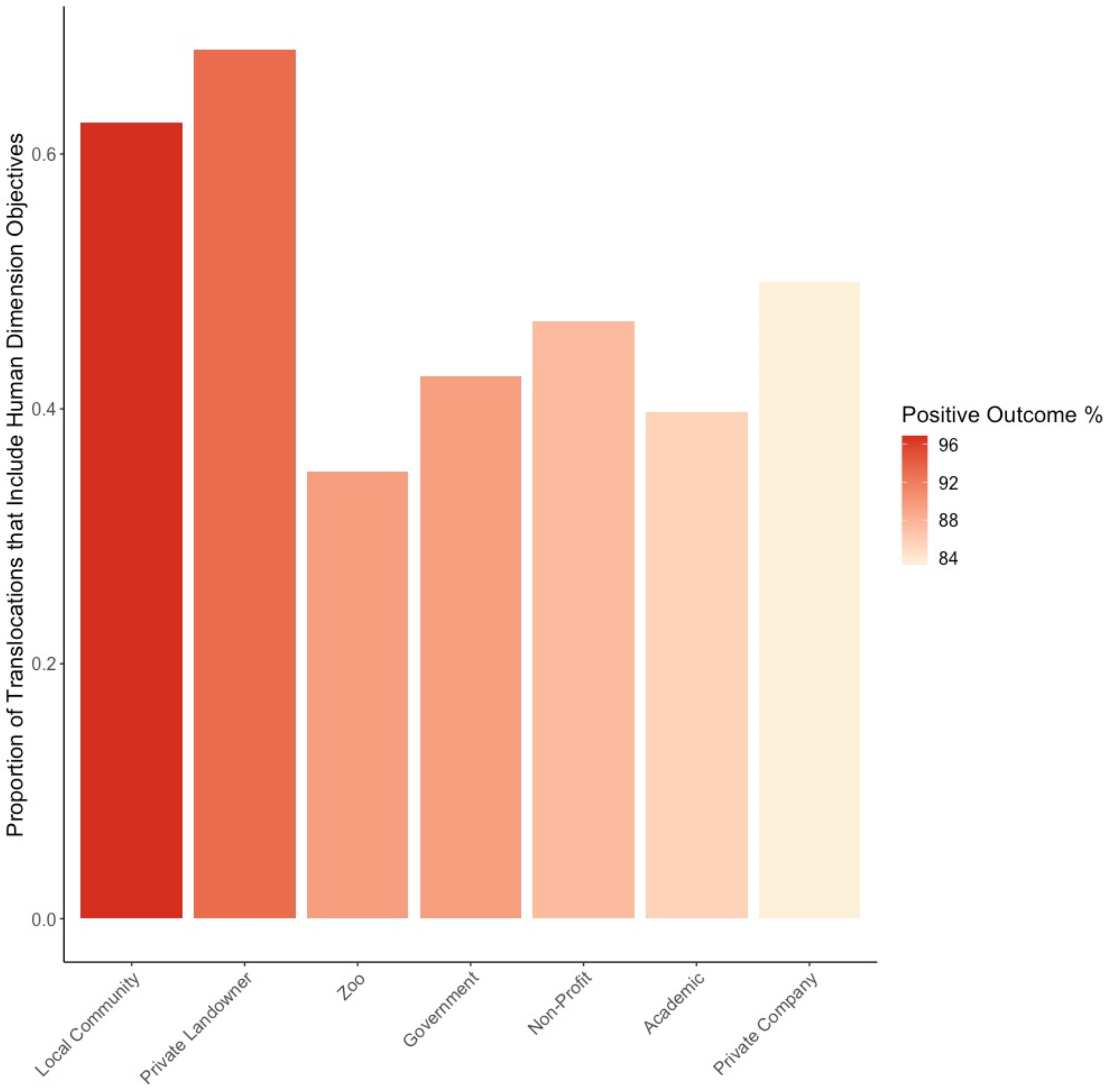


Fig 3. Active inclusion of local stakeholders is linked to improved translocation outcomes. Bars indicate the proportion of studies reported in the IUCN Global Re-introduction Perspectives Series (2008-2021) that incorporated human dimension objectives in their restoration project varied based on the types of groups involved in the project. The color gradient from lighter red (lower) to darker red (higher) represents the percentage of studies involving each group that had positive translocation outcomes, regardless of whether human dimension objectives were included. By group type, the percent of translocations that resulted in a positive outcome were local community: 97%; private landowner: 93%; zoo: 89%, government: 89%; non-profit: 87%; academic: 85%; private company: 83%.

Translocation efforts from the IUCN case studies spanned from 1922 to 2018. However, because the case study from 1922 was an outlier occurring 38 years before any other case study in the dataset, we removed it from the temporal analysis and began instead with a case study from 1960. Since then, the inclusion of human dimension objectives has increased over time from an estimated probability of inclusion of 0.20 (95% CI=0.09-0.40) in 1960 to an estimated probability of inclusion of 0.50 (95% CI=0.40-0.60) in 2018 ($p = 0.05$; Fig. 4). However, there was no significant increase in the inclusion of human dimension objectives following the publication of IUCN Guidelines for Reintroductions and Other Conservation Translocations (before publication, $n = 248$; after publication, $n = 38$; $p > 0.05$).

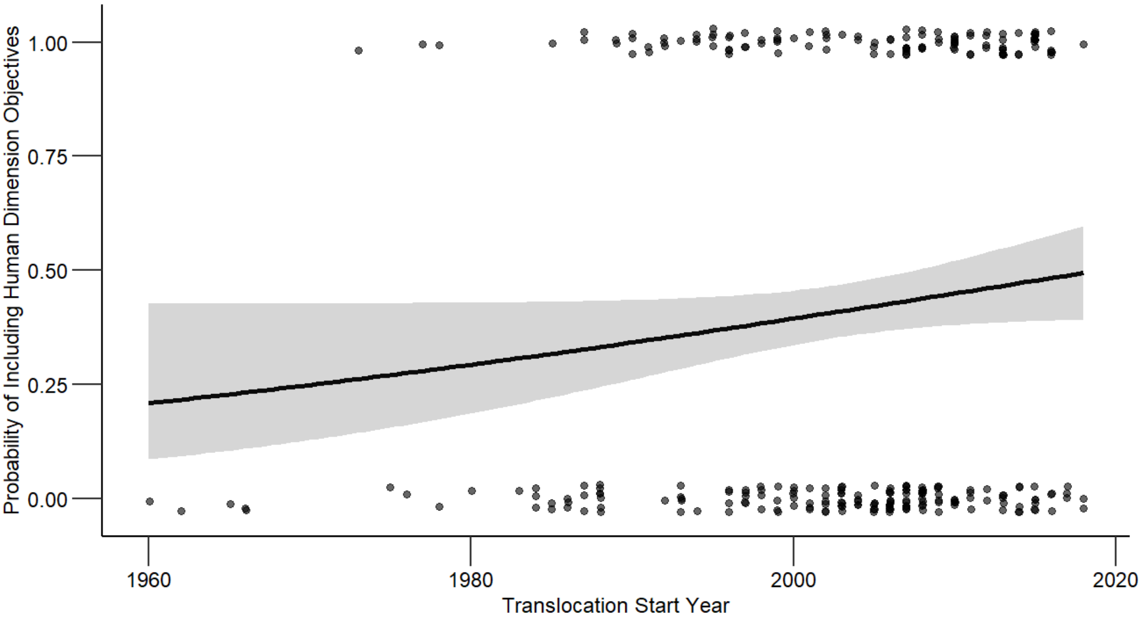


Fig. 4: The inclusion of human dimension objectives has increased over time. The line indicates the predicted probability of including a human dimension objective in a wildlife translocation through time; the shaded area represents the 95% confidence interval, and the points indicate raw data (binary inclusion or exclusion of human dimension objectives). We applied jitter to the points to increase readability. Data source: Global Re-introduction Perspectives Series (2008-2021).

DISCUSSION

Human dimensions are increasingly thought to play a critical role in the success of conservation efforts, and our work supports this assertion by quantifying a strong relationship between the inclusion of human dimension objectives and the probability of success for wildlife translocation projects. Our analysis of all vertebrate case studies reported in the IUCN Global Re-introduction Perspectives Series from 2008 to 2021 revealed projects that included human dimension objectives during the planning process were associated with a 10% higher probability of a positive outcome (i.e., survival, reproduction, and/or growth of a wildlife population) for the wildlife population than those that did not. Our findings therefore reveal opportunities to improve the outcomes of wildlife translocations not only by addressing the environmental and programmatic factors known to influence conservation success, but also by addressing human dimensions through facilitating education opportunities, providing economic benefits, engaging locals in conservation, increasing social tolerance, improving cultural benefits, or enforcing regulations. Our analysis also highlights the importance of engagement and collaboration with local stakeholders by traditional wildlife conservation groups.

Our results suggest that the inclusion of human dimension objectives is biased towards translocations of mammals and, to a lesser extent, birds. It has long been suggested that there is a taxonomic bias towards mammals and birds in conservation research, despite amphibians being more threatened and declining more rapidly than both birds and mammals (Clark & May, 2002; Stuart et al., 2004). A recent analysis identified agriculture, logging, and hunting as the most common threats for amphibians globally, all of which are directly caused by humans (Harfoot et al., 2021). Even so, few amphibian restoration efforts planned for human dimensions, perhaps due to a lower perceived value of this taxa to natural ecosystems and society (Olson & Pilliod, 2022). There may be a number of reasons why translocations of mammals and birds are more likely to incorporate human dimensions. In general, mammals and birds are larger and wider ranging than other taxa, putting them at a greater risk of conflict with humans. Conservationists might be more attuned to this risk, and therefore more likely to include human dimension objectives in related translocation efforts (Carwardine et al., 2019). In addition, methods for including human dimensions like education programs and directly involving community members in restoration efforts might be more straightforward for species considered “charismatic,” which tend to be larger mammals.

Conservationists have long called for more collaborative and bottom-up approaches, like community-based conservation, which center conservation around the needs and wants of local communities (Berkes, 2007). In addition, there is a growing recognition of the value of acknowledging, learning, and integrating critical ecological knowledge of local communities and indigenous groups (Ramos, 2022). In some cases, top-down approaches in wildlife conservation have led to the displacement of local people and increased economic inequality, while providing little to no benefit for local people or even wildlife or ecosystems more broadly (Brockington & Igoe, 2006; Dickman, 2010). These negative experiences may sow distrust and build local resentment to conservation efforts, thereby damaging long-term conservation success (Redpath et al., 2017). Conversely, bottom-up approaches that democratize conservation and prioritize the needs and knowledge of local communities can lead to increased trust, learning, and better outcomes for wildlife conservation (Hazzah et al., 2014; Oldekop et al., 2016; Redpath et al., 2017). Still, many of the translocation projects we reviewed did not include local community groups.

While our results provide clear support for the consideration of people in wildlife translocations, not all human-focused conservation strategies led to better outcomes for wildlife populations. Although conservation-related regulations can serve as an effective tool for improving translocation outcomes, some instances of militarized enforcement has created repressive and violent policies that undermine biodiversity conservation by further alienating local communities (Duffy, 2014). Additionally, while ecotourism and other economic incentives can yield positive conservation results, they can also cause tension among community members around issues of inequitable benefit sharing, ultimately undermining conservation objectives (Hall, 2019). Therefore, the implementation of human dimension objectives must carefully consider all possible social and ecological outcomes, and interdisciplinary science may be key to future restorations.

Only 42% of case studies reported in the IUCN Global Re-introduction Perspectives Series reported human dimension objectives in the planning phase of their projects. Over the last few decades, there have been significant calls to better link conservation goals to sustainability goals, as well as to human values and wellbeing (Berkes, Fikret; Folke, 2000; Lukacs et al., 2020; Manfredo et al., 2021; Ostrom, 2009; Schwartz et al., 2018). Additionally, major national and international conservation initiatives like the Convention on Biological Diversity and California's 30x30 Executive Order aim to center human dimensions in their respective frameworks (Convention on Biological Diversity, 2020; Executive Order N-82-20, 2020). The IUCN Guidelines for Reintroductions and Other Conservation Translocations also has important recommendations for evaluating the social feasibility and conducting socioeconomic risk assessments of translocations (Consorte-McCrea et al., 2022). These advancements have all likely led to the observed increase in reported human dimension objectives. Still, even in the most recent 2021 IUCN report, only 50% of reported translocations set human dimension-related Goals or Success Indicators.

Further highlighting the importance of human dimensions in wildlife translocations, 57% of case studies cited human dimensions as a Lesson Learned or Major Difficulty. In fact, an additional 15% of case studies included human dimensions in either their Lessons Learned, or Major Difficulties Faced compared to their Goals or Success Indicators. In Ireland, inadequate consideration and consultation of a rural farming community prior to the reintroduction of the white-tailed eagle (*Haliaeetus albicilla*) resulted in widespread poisoning and high eagle mortality (O'Rourke, 2014). Future translocations should utilize conservation planning tools that integrate both ecological and socioecological variables which have been found to better predict the expansion of recolonizing wildlife populations, the occurrence of human-wildlife conflict, and effective release sites for reintroduced individuals (André et al., 2022; Behr et al., 2017; McCann et al., 2021).

Education and outreach were the most commonly reported human dimension strategy incorporated in translocation project planning. Importantly, education and outreach can help introduce people to the species and the goals of the project, as well as influence the behavior of the general public (George & Sandhaus, 2013). For example, conservationists who reintroduced the critically endangered Pahrump poolfish (*Empetrichthys latos*) in Nevada largely attributed their success to increased public buy-in following an education and media campaign (Soorae, 2021) (Fig. 4). Other popular human dimension objectives include increasing social tolerance and providing economic benefits to aid biodiversity conservation efforts (Ando & Langpap, 2018; Carter & Linnell, 2016). In Chile, wildlife tourism of an increasing puma (*Puma concolor*) population has led to a sharp decline in support for the lethal control of pumas, the primary cause of their decline and extirpation throughout the region (Ohrens et al., 2021). Interestingly, enforcement was one of the least commonly reported strategies despite increasing global attention to anti-poaching and wildlife trafficking efforts (Duffy, 2014). Future analyses that further disentangle the effectiveness of various strategies may aid in increasing the implementation of human dimensions by conservation organizations.

Our analysis is just the beginning of better understanding how human dimensions impact the success of wildlife restorations globally. We note that our binary classification of outcomes solely focuses on the outcome to the population of the species as stated by the authors, so it does not account for success related to knowledge gained for future restorations, stakeholder support, or other non-population related successes. Further, our results may be influenced by reporting bias against translocations conducted by smaller organizations as well as translocation failures. The publication rate for successful translocations is likely to be higher as many failed translocations are underreported (Miller et al., 2014) which may partially account for the low failure rate (11%) in the IUCN report. Thus, our analysis is representative of the literature, but not all attempted translocations. Still, we've found that major, well-resourced conservation organizations and relatively overreported successful translocations are failing to incorporate human dimensions into their efforts; this speaks particularly strongly to the overall lack of consideration for human dimensions if arguably the best-resourced and most successful translocations are foregoing important opportunities to improve conservation outcomes and local partnerships.

Effective wildlife translocation clearly requires thoughtful consideration of the human dimensions that make conservation projects more sustainable and successful. As biodiversity continues to decline, there is an urgent need to integrate well-established biological and environmental schema with a deeper understanding of the social and human dimensions that will help to avoid unaffordable failures. A single wildlife restoration failure can result in a species' extinction (Hilbers et al., 2020; Jachowski, David S.; Millspaugh, Joshua, J.; Angermeier, Paul, L.; Slotow, 2016), as well as the loss of millions of dollars and the sowing of distrust between communities and conservation institutions. Therefore, analyses to understand even marginal gains in translocation success can be impactful for future conservation efforts. Tools and practices to better understand the human dimensions of translocations like stakeholder engagement or participatory approaches can be both costly and time consuming, yet our study underscores their importance. While the literature is ripe with frameworks and guidelines that emphasize the need to include human dimensions, too few projects adequately plan for the human dimensions needed for long-term success (Batson et al., 2015; IUCN/SSC, 2013).

Chapter 3. Behavioral state-dependent selection of roads by guanacos

This chapter is in press and is included here with permission from co-authors.

Serota, M.W., P.A.E. Alarcón, E. Donadio, A.D. Middleton. Behavioral state-dependent selection of roads by guanacos. *Landscape Ecology*.

ABSTRACT

Widespread globally, roads impact the distribution of wildlife by influencing habitat use and avoidance patterns near roadways and disrupting movement across them. Wildlife responses to roads are known to vary across species; however within species, the response to roads may depend on the season or the individual's behavioral state. We assess the movement behavior and space use of the most widespread large herbivore in Patagonia, the guanaco (*Lama guanicoe).* We estimated the preference or avoidance to paved or unpaved roads (the proximity effect) and the preference or avoidance to traverse them (the crossing effect). Using GPS collar data, we combined Hidden Markov Models with an integrated step selection analysis to segment guanaco movement trajectories into individual behaviors and test for differences in road effects on movement. We found that guanacos display distinct movement responses to different types of roads depending on their behavioral state. Guanacos select for proximity to paved roads while foraging, but against them when traveling. Yet, guanacos select for unpaved roads when traveling. Despite the selection for proximity to paved roads, guanacos avoid crossing them, irrespective of their behavioral state. Our findings offer significant implications for guanaco distribution and management across Patagonia. The selection for roads strongly influences the distribution of guanacos, which could concentrate grazing in some areas while freeing others. Despite potential benefits such as increased vegetation near roadsides, increased association with roads while foraging may result in an ecological trap. Finally, the strong aversion to crossing paved roads raises concerns about habitat loss and connectivity.

INTRODUCTION

Animal movement is driven by the spatiotemporal distribution of resources as individuals search for food, acquire mates, and seek safety (Nathan 2008). However, anthropogenic changes, such as habitat loss, energy development, and climate change, are rapidly creating novel landscape conditions that impact animal's resources (Chambers et al. 2022; Pike et al. 2023). In response to these changes, animals may need to adapt and adjust their behavior and movement patterns to survive. Human activities can also create both physical barriers, like fences and dams, as well as perceived barriers due to fear of human persecution. Barriers that impede movement can lead to a diminished capacity to track essential resources, thereby resulting in individual fitness consequences, a decline in population connectivity, and a reduced flow of nutrients across an ecosystem (Tanner and Perry 2007; Holderegger and Di Giulio 2010; Bauer and Hoye 2014). Therefore, it is crucial to understand how human activities reshape the resource landscape while also recognizing their potential to restrict animal movement.

Spanning over 21 million kilometers, roads are amongst the most widespread anthropogenic features on landscapes around the world (Meijer et al. 2018). The population impacts of roads on wildlife, like road-related mortality, are well documented. Vehicles cause 7% of mammal, 13% of reptile, and 4% of amphibian mortality worldwide (Hill et al. 2019). As a dominant feature on the landscape, roads can also influence wildlife behavior through habitat modification that drastically changes conditions like light and soil characteristics impacting animal foraging, breeding, and predator avoidance strategies (Teixeira et al. 2020; Hill et al. 2021) . These changes to the resource landscape can lead to alterations in habitat selection through road avoidance or attraction. The proximate causes of road avoidance varies from species to species as some individuals may be avoiding increased noise, differences in habitat quality, or even changes to the microclimate (Ortega and Capen 1999; McClure et al. 2013). Conversely, other species may select for habitat near roads due to increasing plant productivity, refuge from predation, thermoregulation, or the facilitation of movement (Hill et al. 2021). Roads can also impact habitat selection by impeding movement as some species avoid crossing them (Brehme et al. 2013; Aiello et al. 2023). Responses to roads can vary across species, but also within the same species. Individual decisions to associate with or avoid roads may be influenced by seasonal variations or their current behavioral state (resting, foraging, or traveling), potentially reflecting the influence of distinct proximate mechanisms underlying these movement patterns. Some individuals might be attracted to roads when traveling due to a reduction in energy costs, while that same individual might be repulsed by roads when foraging if there is better quality forage away from roads. Roads undoubtedly impact wildlife, however these impacts may be more dynamic than previously appreciated.

Guanacos (*Lama guanicoe*) are the most widespread large herbivore in Patagonia, but land-use change, overhunting, and competition with livestock drove their populations to approximately 3-7% of their original abundance by the early 20th century (Baldi et al. 2016). Roads are a potential threat to remaining guanaco populations. Previous research suggests that guanacos are negatively affected by roads both directly, via vehicle collisions and roadside fence entanglements, and indirectly, as roads provide hunters easy access to guanacos (Rey et al. 2012; Radovani et al. 2014). Still, studies looking at the effects of roads on guanaco abundance and distribution have found mixed results (Cappa et al. 2017, 2019; Schroeder et al. 2018). In La Payunia Reserve, unpaved roads were found to have no effect on guanaco abundance (Schroeder et al. 2018). However, guanaco responses to roads may differ based on the road type. Unpaved dirt roads have lower traffic volume and speed, and potentially offer easier travel for guanacos. However, this easier travel may come at a cost of increased accessibility for poachers and hunters. In contrast, paved roads, while posing risks from high-speed traffic, can significantly alter the physical terrain, potentially facilitating water accumulation and plant growth that could attract guanacos. One study in northern Argentina found a greater abundance of guanaco dung piles near unpaved roads than paved roads, potentially indicating that paved roads negatively affect guanaco distribution (Cappa et al. 2019). Still, it is unclear how both paved and unpaved roads impact guanaco behavior, whether they attract or repel guanacos, and how they may act as barriers to movement. Understanding this behavior is particularly important as guanaco population estimates almost entirely rely on road-based surveys. The attraction or avoidance of roads can introduce substantial bias, jeopardizing the accuracy of these estimates.

In this study, we integrate multiple animal movement analyses to evaluate guanaco habitat use and movement behavior near both paved and unpaved roads (i.e., proximity effect), and to understand how roads influence movement across roads (i.e., crossing effect). The proximity effect is the probability of using habitat as a function of distance to the road, whereas the crossing effect assesses the permeability of the road. Further, because guanaco behavioral responses may be mediated by their behavioral state or by seasonality, we analyzed the effects of roads separately by season (spring-summer vs. autumn-winter) and behavioral state (resting, foraging, and traveling). We hypothesized that roads will impact the habitat selection of guanacos, but only during specific behavioral states. Specifically, we predict that guanacos would select for roads while foraging due to greater primary productivity all year round, but selection for roads will be stronger for paved roads in the spring and summer months when there is less water availability for plant growth. In addition, we predicted that guanacos would avoid paved roads when traveling due to high traffic volume and select unpaved roads, as they may facilitate less energetically demanding movement. Finally, again due to the variation in traffic volume, we predict that guanacos would avoid crossing paved roads but would readily traverse unpaved roads. We do not expect these patterns to change seasonally.

METHODS

Study Area

Established in 2004, MLNP is located on the east coast of Argentina within the Santa Cruz province, covering 61,000 hectares and 30 kilometers of coastline (Fig. 1). The park is characterized by coastal steppe with both shrubland and grassland ecosystems. Black shrub (*Junellia tridens)* and pine-scented daisy (*Lepidophyllum cupressiforme),* dominate the shrublands, while thatching grass (*Festuca pallescens), salt grass (Puccinellia* sp.), bentgrass (*Agrostis* sp.), and coast tussock-grass (*Poa atropidiformis)* dominate the grasslands (Oliva et al. 2006). Average annual precipitation is 255 mm, characterized by rainfall during the autumn-winter months (April-September) and a dry season in spring-summer (October-March) (Paruelo et al. 1998). Average temperatures are 4.7 °C during the autumn-winter months and 13.8 °C during the spring-summer months. Therefore, we split our data into two distinct periods, the autumn-winter months (April-September) with lower temperature and more precipitation and the spring-summer months (October-March) with higher temperatures and lower precipitation.

Some guanaco populations are beginning to recover in Patagonia due to the creation of protected areas and the abandonment of ranches in the region (Carmanchahi and

Lichtenstein 2023). Monte León National Park (MLNP) is one key area where guanaco populations are thought to be recovering and is one of the few places in their range without hunting and competition with livestock (Walker and Novaro 2010). The park is bordered by a major, heavily used state highway, Ruta 3, that separates the park from neighboring ranches. Near MLNP, guanacos are often observed both on and alongside the paved highway.

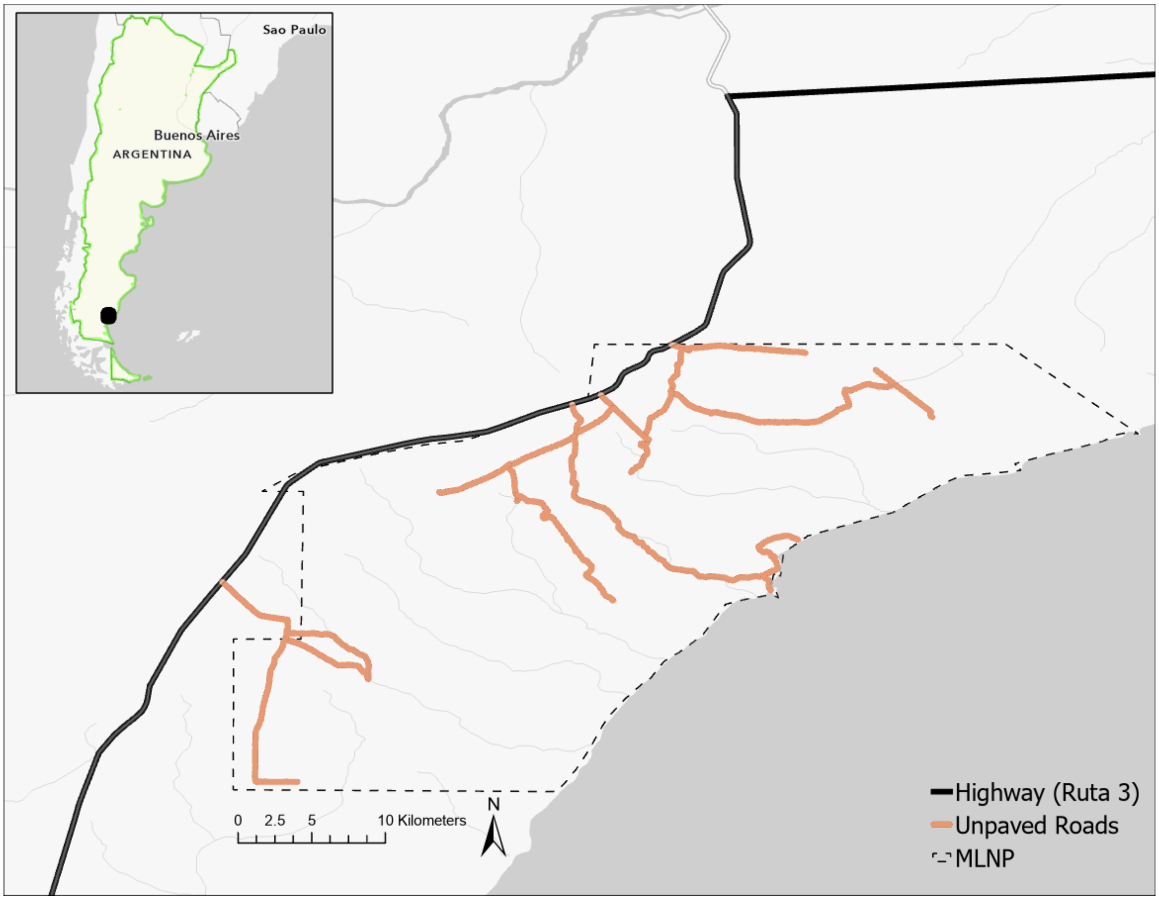


Fig 1 Map of Monte León National Park (MLNP) and location of highway (Ruta 3) and unpaved roads within the park. Inset map includes Argentina and a black dot representing the location of MLNP

GPS Collar Data

From 2019 to 2022 we monitored 29 adult guanacos (14 males and 15 females) during the spring-summer season and 28 (14 males and 14 females) during the autumn-winter season in Monte León National Park in Southern Argentina following all National Park regulations and protocols (Supplementary Table 1). Each GPS collar (LiteTrack Iridium 420, Lotek, Ontario, Canada) was programmed to capture one fix every two hours. For all subsequent analyses, we included GPS locations from collars that recorded data for a minimum of four months between 2019 and 2022. We treated each year of monitoring for individual guanacos as separate individuals (referred to as a guanaco year) to account for changing habitat conditions between years of study (Prokopenko et al. 2017). Multiple guanacos were monitored in more than 1 year of the study resulting in 58 guanaco-years for the spring-summer season and 57 guanaco-years during the autumn-winter season. Fieldwork was conducted under permit IF-2019-111378017-APN-DRPA#APNAC and subsequent renewals issues from the National Park Administration of Argentina (Administración de Parques Nacionales), and UC Berkeley IACUC Protocol # AUP-2019-10-12628.

Behavioral Segmentation

We fit Hidden Markov Models (McClintock and Michelot 2018) to segment guanaco trajectories into distinct behavioral states, based on modeled step lengths and turning angles. Step lengths were modeled using a gamma distribution, while turning angles were modeled using a Von Mises distribution (Langrock et al. 2012). For the initial parameter values, we defined three behavioral states: a resting state characterized by short step lengths (gamma distribution with a mean of 20 m and a standard deviation of 20 m) and uniform turning angles (Von Mises distribution with a mean of π and a concentration of 0), a foraging state with medium-sized step lengths (gamma distribution with a mean of 350m and a standard deviation of 350m) and uniform turning angles (Von Mises distribution with a mean of π and a concentration of 0), and a traveling state with large step lengths (gamma distribution with a mean of 1,500m and a standard deviation of 1,500m) and directed movement (Von Mises distribution with a mean of 0 and a concentration of 1.5). We then assigned each step to the most probable behavioral state using the Viterbi algorithm based on the results of the HMM. This analysis was conducted using the momentumHMM package (McClintock and Michelot 2018) in the R programming language.

Environmental Covariates

Roads for our analysis were both downloaded from publicly available datasets and hand digitized. Ruta Nacional 3 (“Ruta 3”) is a major transportation corridor for Argentina that stretches from Buenos Aires to Tierra del Fuego. Geospatial data for Ruta 3 was downloaded from The World Bank (https://datacatalog.worldbank.org/search/dataset/0038248). For the unpaved roads, we hand digitized roads using satellite imagery and supplementary information from Administración de Parques Nacionales. The roads were categorized into two classes: highways, which are major roads characterized by high speeds and heavy traffic volume, and unpaved roads, comprising unpaved and gravel roads that traverse the park with minimal usage. Traffic for both Ruta 3 and the unpaved roads changes from season to season, with traffic increasing during the spring-summer months. Still, as a major shipping route, Ruta 3 remains heavily trafficked throughout the year. Further, while tourist visitation to the park increases during the summer, visitation is relatively low. We included two additional environmental covariates in our habitat selection model (see below), the terrain ruggedness index (TRI) and the Normalized Difference Vegetation Index (NDVI), in our modeling framework. To calculate a terrain ruggedness index (TRI), we downloaded NASA’s STRM 30m Digital Elevation Model from Google Earth Engine and calculated TRI from the *terrain* function in R. Finally, using the *rgee and reticulate* package in R, we matched each GPS location with the closest 30m spatial resolution

Landsat 8 image (every 16 days) and calculated the Normalized Difference Vegetation Index.

Roadside Fencing

Roadside fences are commonly deployed worldwide along high-traffic, high-speed roadways to prevent wildlife collisions and demarcate borders or private property. In some cases, these fences may exacerbate the barrier effect of large roadways (McInturff et al. 2020). Assessing the individual effects of each feature becomes challenging due to the close proximity of these fences to the road (Jones et al. 2022). Further, at a 2-hour fix rate, the barrier effect observed is at a coarser scale and may miss occasions at which individuals quickly cross back and forth between barriers. At MLNP, our GPS data revealed that after crossing the roadside fence, guanacos crossed back over the fence without crossing the road 65% of the time. In our study, we treat Ruta 3 and the roadside fence as a unified barrier.

Habitat Selection

We used a series of integrated step selection analyses (iSSA) to compare the GPS relocations of guanacos (i.e., used locations) with available locations to estimate relative probability of use for each behavioral state (Avgar et al. 2016; Picardi et al. 2021). To evaluate habitat selection, we divided the data based on behavioral state (resting, foraging, and traveling) and season (spring-summer and autumn-winter). We generated 10 random steps for each used step by randomly selecting the step length and turning angles from a gamma and von Mises distribution (Avgar et al. 2016). The gamma and von Mises distributions were generated separately for each individual and behavioral state, and parameterized based on the empirical distribution of used step lengths and turning angles of that individual. For each model, we included consistent core environmental covariates expected to influence guanaco habitat selection regardless of road effects (Prokopenko et al. 2017; Londe et al. 2022). Our selection of environmental variables was informed by previous research on guanaco habitat selection, which emphasized the importance of ruggedness and forage availability (Verta 2022). Both forage availability (here estimated by NDVI) and terrain ruggedness have been found to be important predictors of guanaco movement and distribution in several studies (Marino and Baldi 2008; Pedrana et al. 2010; Flores et al. 2012; Smith et al. 2020; Verta 2022). For NDVI, we also included a quadratic term as individuals may be selecting for more intermediate values of forage (Verta 2022). These covariates were estimated at the end of each individual step. In all models we also included the step length, the logarithm of step length, and the cosine of the turning angles as covariates to account for the movement process (Avgar et al. 2016). Lastly, COVID-19 led to widespread restrictions in vehicular traffic in Argentina from April 2020 until November 2020, so we included an interaction term for the months with restricted traffic due to COVID-19 on our proximity and crossing variables.

To model selection of proximity to each road type, we included a variable for the distance to a highway and unpaved road at the end of a random or observed step. This variable assumes that if a road influences selection, individuals will, on average, select steps that end either closer to or farther away from the road compared to what would be expected randomly. For each distance variable, we used a decay function, with α set to 1000 m, to account for a decreased behavioral response further from the road (Carpenter et al. 2010). Further, we separately modeled a crossing effect for both road types. We created a crossing covariate by tracing movement paths from each point (used and available) to the last point. We separated models containing road proximity covariates and road crossing covariates, as their simultaneous evaluation within a single model is discouraged due to collinearity (Prokopenko et al. 2017; Jones et al. 2022; Londe et al. 2022). Prior to modeling by season and state, we employed model selection with Akaike's information criteria (AIC) evaluation for all covariate combinations, finding that the full model with all environmental and road variables yielded the lowest AIC score (for details see Supplementary Table 2). Therefore, we included all covariates for subsequent modeling by season and behavior.

We built mixed conditional logistic regression models for each model by state and season, with strata for each pairing of used and available locations and guanaco year as a random effect. All covariates were scaled and centered. We defined each model using the R package *glmmTMB* to allow for each guanaco year as a random effect (Brooks et al. 2017). We evaluated the support for each fixed effect by examining the 95% confidence intervals, and we interpreted variables with confidence intervals that did not overlap zero as significant. We also calculated the Variance Inflation Factor for each variable to ensure an acceptable level of collinearity (VIF < 4.0 for all predictors in each model). Lastly, we evaluated the performance of each model by calculating the continuous Boyce index which compares the predicted values with expected values across the study area (Hirzel et al. 2006). Values for the continuous Boyce index range from 0 to 1 with values closer to 1 indicating better model performance.

RESULTS

The average number of relocations varied across seasons with each guanaco having on average 1,982 (SD = 1,131) observed steps in the spring-summer season and 1,971 (SD = 1,267) observed steps in the autumn-winter season. Estimated mean step length (SD) was 10 (7) m for the resting state, 266 (231) m for the foraging state, and 1,012 (811) m for the traveling state (Supplementary Material Figures 1, 3, and 5). Turning angle distribution (concentration parameter) had an estimated mean of 3.11 (0.34) for the resting state, 2.95 (0.02) for the foraging state, and 0.04 (0.87) for the traveling state (Supplementary Material Figures 2, 4, and 6l). Overall, using the Viterbi Algorithm, guanacos were resting 28% of the time, foraging 48% of the time, and traveling 24% of the time. During the daytime guanacos were resting 1% of the time, foraging 60% of the time, and traveling 39% of the time. However, during the nighttime, guanacos were resting 55% of the time, foraging 36% of the time, and traveling 9% of the time. During the spring-summer period, guanacos were resting 21% of the time, foraging 56% of the time, and traveling 23% of the time. Similarly, during the winter-autumn period, guanacos were resting 36% of the time, foraging 42% of the time, and traveling 22% of the time.

During the spring-summer season, guanacos had 4,961 (8%) and 41,389 (67%) observed steps within 1 km of the highway and unpaved roads, respectively (Fig. 2). During this time, guanacos crossed the highway a total of 101 times and unpaved roads 5,899 times. During the autumn-winter season, guanacos had 6,424 (10%) and 31,358 (59%) observed steps within 1 km of the highway and unpaved roads, respectively. During this time, guanacos crossed the highway a total of 51 times and unpaved roads 3,345 times. Proximity to the highway was not contingent on the time of day, with 56.1% of the observed steps within 1km of the highway occurring during the day and 43.9% at night. Likewise, proximity to unpaved roads was not dependent on the time of day, with 54.6% of the observed steps within 1 km of unpaved roads occurring during the day and 45.4% at night. There were 2,497 GPS points within one average step length (245m) of the highway, and of all those points, 2,401 points (96%) were on the parkside. There was considerable individual variation as the maximum number of highway crossings observed by an individual was 35, while the minimum was 0, and the median was 2. Six individuals never crossed the highway. Of the 152 times guanacos crossed the highway, they crossed back within 24 hours 88% of the time (n = 133).

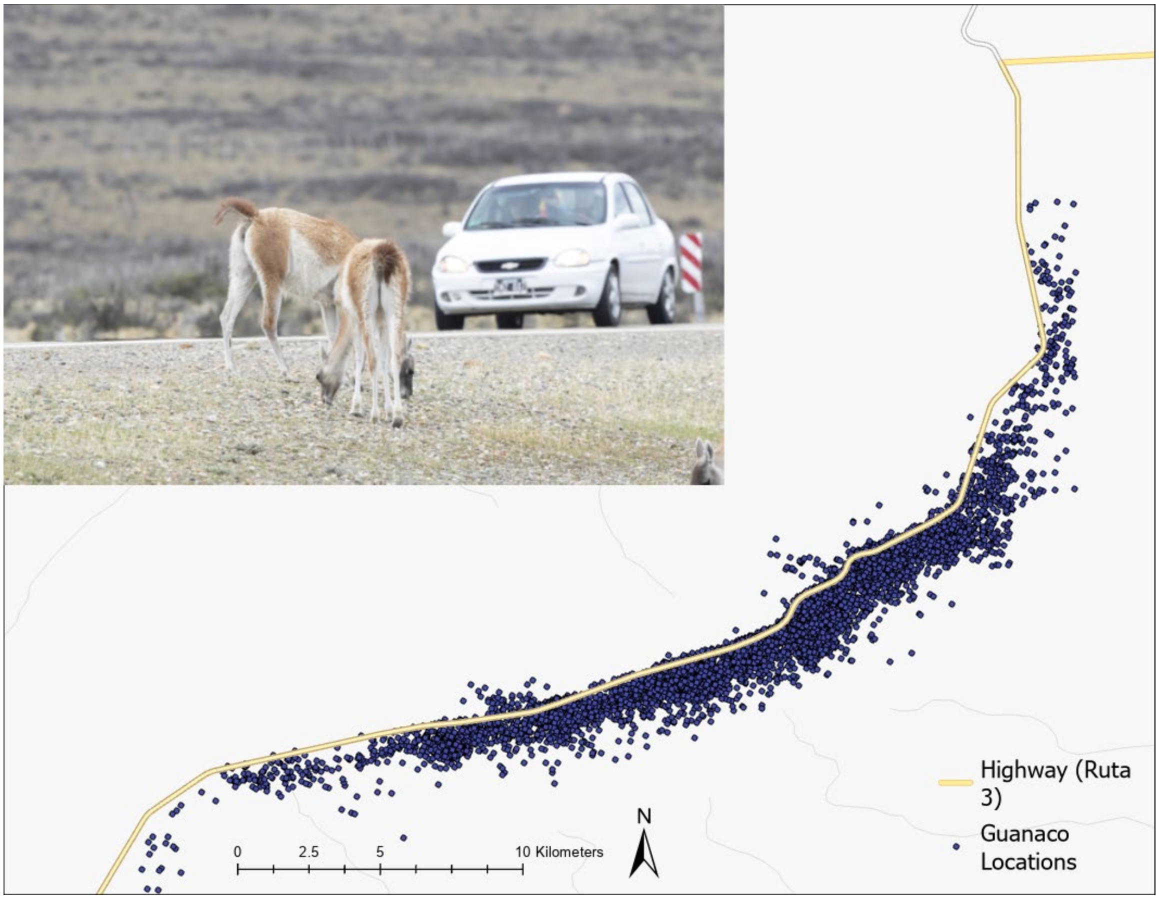


Fig. 2 Guanacos foraging along the highway (Ruta 3). All GPS locations within 1 km of the highway east and every GPS location west of the highway. Parque Nacional Monte León, Santa Cruz Province, Argentina

Model parameter estimates for the proximity model differed by behavioral states and season (Fig. 3). The interaction term between the COVID-19 months and the proximity and crossing variables was not significant in all models and was therefore removed ($p > 0.05$ in all cases). In a resting state, guanacos only selected for proximity to unpaved roads during the autumn-winter season (autumn:winter 95% CI 0.01 - 0.04). In a foraging state, guanacos selected for proximity to highways in both seasons (spring:summer 95% CI -0.06 - -0.04 and autumn:winter 95% CI -0.03 - -0.01), but only selected for unpaved during the spring-summer season (spring:summer 95% CI -0.03 - -0.01). However, in a traveling state, guanacos selected against proximity to highways in both seasons (spring:summer 95% CI: 0.04 - 0.09 and autumn:winter 95% CI: 0.20 - 0.70), and for proximity to unpaved roads (spring:summer 95% CI -0.08 - -0.03 and autumn:winter 95% CI -0.04 - -0.01).

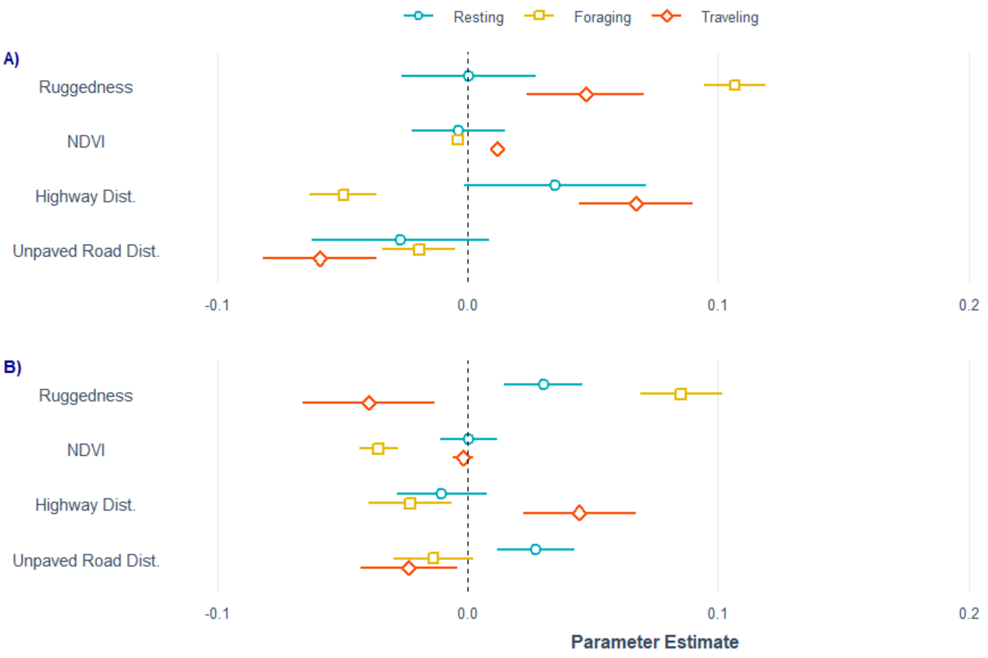


Fig 3 Spring-summer (A) and autumn-winter (B) proximity model parameter estimates by separate behavioral state models. Parque Nacional Monte León, Santa Cruz Province, Argentina

Model parameter estimates for the crossing model also differed by behavioral state and season (Fig. 4). Due to the short step lengths of the resting state, only 1 available step crossed the highway. Therefore, the crossing model for the resting state during both seasons failed to converge. During the foraging state, guanacos selected against crossing the highway during both seasons (spring:summer 95% CI -1.55 - -0.99 and autumn:winter 95% CI -2.20 - -1.42) and unpaved roads during the spring-summer season (95% CI -0.12 - -0.04). Similarly during a traveling state, guanacos selected against crossing the highway during both seasons (spring:summer 95% CI -2.10 - -1.51 and autumn:winter 95% CI -2.70 - -1.98), but showed no selection for or against crossing unpaved roads.

Fig 4 Spring-summer (A) and autumn-winter (B) crossing model parameter estimates by separate behavioral state models. Parque Nacional Monte León, Santa Cruz Province, Argentina

Finally, each model had a relatively high predictive performance (Hirzel et al. 2006). The continuous Boyce index values were all higher than 0.70 (Supplementary Table 3).

DISCUSSION

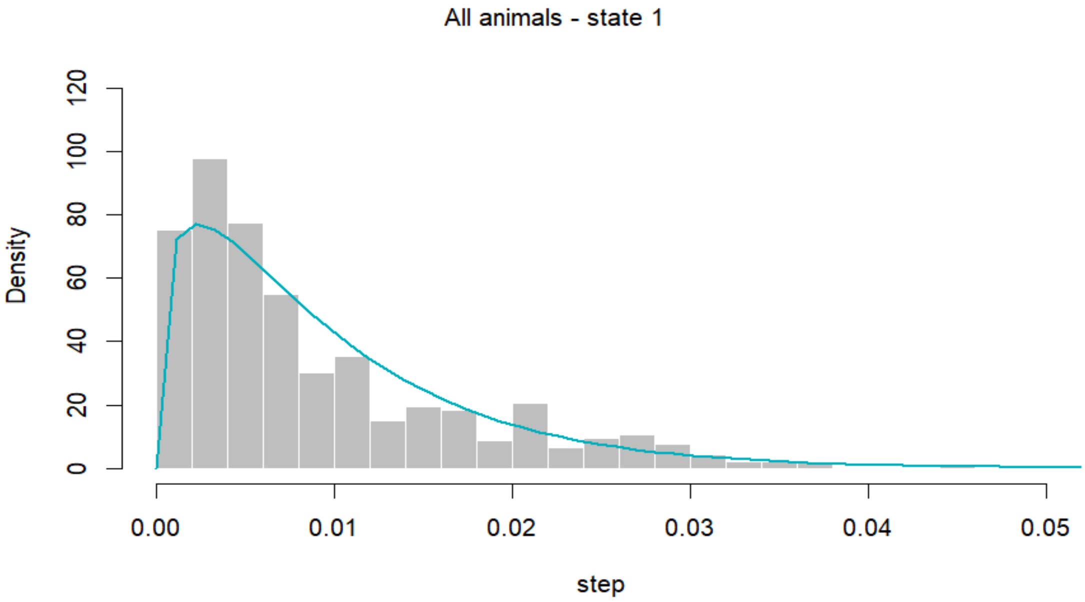
Roads are among the most prominent anthropogenic features on the planet, yet their impact on wildlife can be difficult to discern because it can vary by species, behavioral state, and season. Our findings indicate that the guanaco, the most widespread large herbivore in Patagonia, responds differently to different types of roads based on their behavioral state. When foraging, guanacos selected strongly for highways. However, when traveling, guanacos selected for unpaved roads and against highways. Despite strong selection for highways when foraging, guanacos consistently avoided crossing them. The aversion to crossing highways was observed regardless of their behavioral state. Combined, the strong selection of proximity to highways while foraging and the avoidance of crossing them, drastically impact guanaco behavior. This pattern could have substantial effects on guanaco distributions throughout Patagonia, with potential implications for the conservation and management of this species.

We found that guanacos selected for roads, particularly while they are foraging. Guanacos may be foraging near roads to capitalize on the facilitation of foraging opportunities provided by the presence of roads. Roads can have significant impacts on vegetation patterns and productivity, and these effects may be more pronounced in semi-arid and arid ecosystems. In these environments, where water is typically a limiting factor for plant growth, the runoff water from roads can enhance vegetation productivity, resulting in patches of more abundant and diverse vegetation along road edges (Dean et al. 2019). Plant communities alongside roads may also include more introduced species that green up faster than the surrounding landscape (Roever et al. 2008). Additionally, the concentration of total dissolved nitrogen can be higher near roads. Therefore, changes to vegetation productivity and quality may result in increased selection of habitat near roads. In the semi-arid saltbrush steppe of Australia, kangaroos are attracted to roads during drought years when resources are scarce (Lee et al. 2004; Klöcker et al. 2006). Guanacos in Patagonia, however, appear to be consistently attracted to the highway while foraging throughout the year. Further, some species may associate with roads to avoid predation (Hill et al. 2021). Across their range, pumas, the main predator of guanacos at MLNP, are thought to mostly avoid high-use, paved roads (Dickson et al. 2005; Caruso et al. 2015). Despite potential anti-predator benefits, the scarcity of guanaco sightings near roadsides at night suggests road association is unlikely to be driven primarily by predator avoidance. Ultimately, the proximate mechanism for this behavior is still not well understood and future work should test for differences in nutrient availability or minerals in plants along the road to better understand if differences in forage availability results in increased selection of roads.

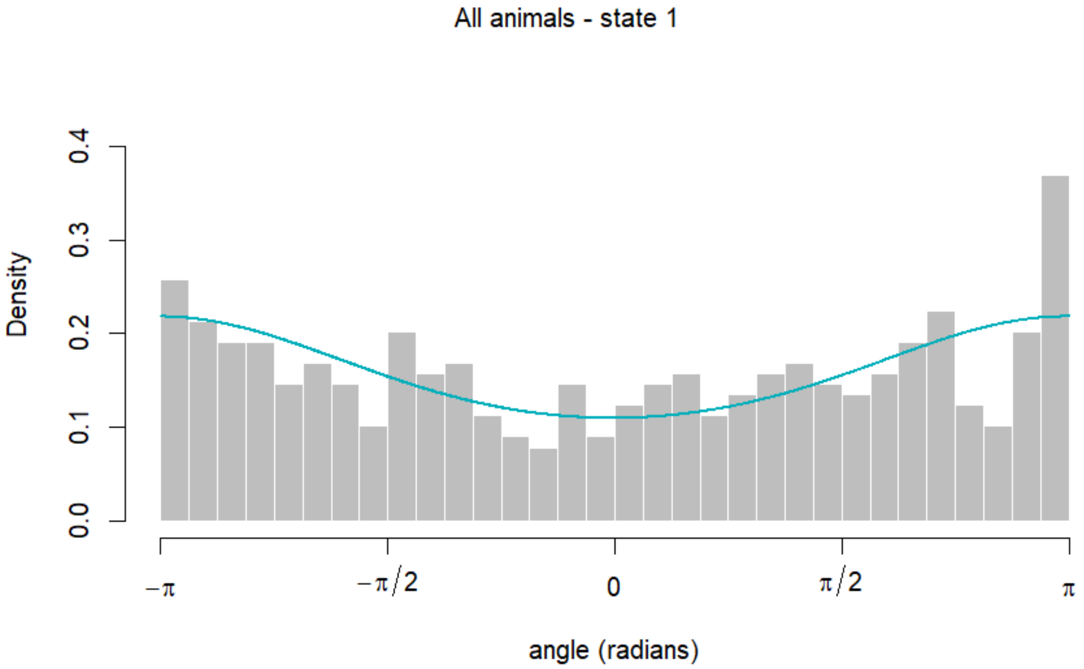
Although guanacos forage near highways, they consistently avoid crossing them, indicating that highways serve as significant barriers to their movement. Ruta 3, the highway bordering MLNP, is a heavily trafficked transportation and shipping route frequented by freight trucks. Throughout the length of the study, we observed very few instances in which guanacos crossed the highway. However, around MLNP and other areas with high densities of guanacos, it is very common to see individuals walking on the highway. So, given our 2-hour fix rate, it is likely that we missed events in which guanacos quickly crossed the highway, but then crossed back. Still, guanaco locations within an average step length of the highway were concentrated in the parkside (96%), suggesting minimal crossing events. It is widely known that roads can be barriers to movement for wildlife, hence the proliferation of road crossing structures in recent years (Smith et al. 2015; Sijtsma et al. 2020). However, considering the strong preference for roads while foraging, the extent of the barrier effect on guanaco movement is surprising. The ultimate explanation for this barrier effect is still not fully understood. Factors such as high traffic volume and roadside fencing are both commonly cited reasons for road avoidance and likely deter some individual guanacos from crossing (Jacobson et al. 2016). However, if individuals are crossing short spatiotemporal scales but returning to the park side of the road, it could indicate lower vegetation quality in ranchlands or the avoidance of private lands due to fear of persecution as potential drivers of this behavior. In fact, previous studies, for example, have found that guanacos have increased flight behavior where hunting pressure is high (Donadio and Buskirk 2006). A barrier effect that limits guanaco space use is a major concern, so further unpacking whether the driver of this barrier is traffic, roadside fencing, forage availability in neighboring ranches, or other human influences may be critical for future guanaco conservation efforts (Puig et al. 1997; Schroeder et al. 2014).

The road-induced impacts on guanaco behavior requires further investigation to mitigate potential management and conservation challenges. First, while the attraction of guanacos to roads can benefit some individuals, it can also result in an ecological trap, leading to detrimental consequences for individuals and populations. For other species, increased association with roads can lead to increases in vehicle collisions, poaching, exposure to heavy metals, noise pollution, and artificial light (Frangini et al. 2022). Second, increased association with roads may contribute to both a public perception of guanaco overabundance and skewed population estimates by managers, potentially leading to the mismanagement of this species. Throughout Patagonia, sheep ranchers are increasingly concerned about the recovery of some guanaco populations due to potential competition with livestock, and many believe that current populations are overabundant, beyond carrying capacity, and contributing to a decline in the profitability of livestock husbandry (Flores et al. 2023). In response to concerns about declining productivity, the Santa Cruz province implemented a resolution in 2023 that increased the daily guanaco harvest quota from 1 to 2 animals per hunter (El Consejo Agrario Provincial de Santa Cruz 2023). Regular sightings of guanacos along the roadside may be influencing the public perceptions of these animals, fueling a bad reputation of this camelid in the region. In addition to local perceptions of guanaco overabundance, the attraction to roads may also be contributing to inaccurate population estimates. Due to their cost-effectiveness and ability to be easily repeated, ground transect surveys conducted along both paved and unpaved roads are the main methodology used for estimating guanaco population densities (Baldi et al. 2001; Travaini et al. 2007, 2015; Pedrana et al. 2010; Marino et al. 2014; Zubillaga et al. 2018). Even in MLNP, population estimates for guanacos are conducted from roads. However, a major assumption of population estimates from road surveys is that the impact of roads on the target species distribution is negligible. Therefore, it’s possible that population estimates for guanacos in MLNP and other regions where guanacos are drawn to roads may be inflated. An overestimation of the guanaco population can have direct impacts on harvest and other wildlife policies, so park managers and researchers should explore other options to measure their densities (e.g. drones, or ground surveys away from roads) to ensure accurate assessments of guanaco populations and informed wildlife management policies.

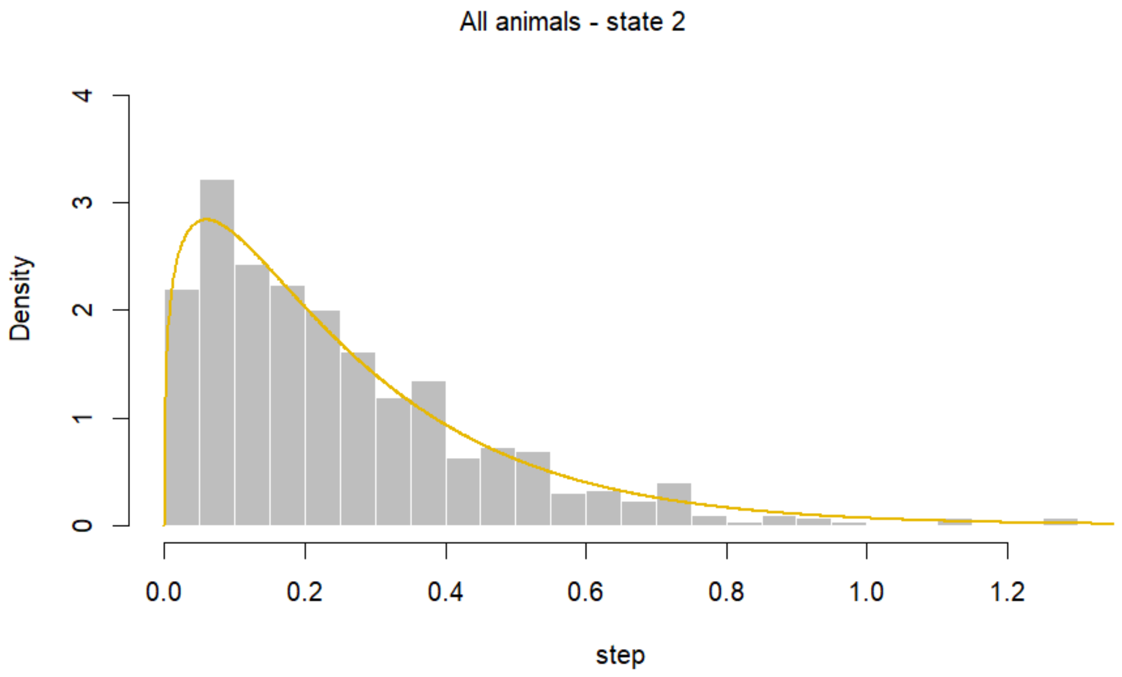
SUPPORTING INFROMATION



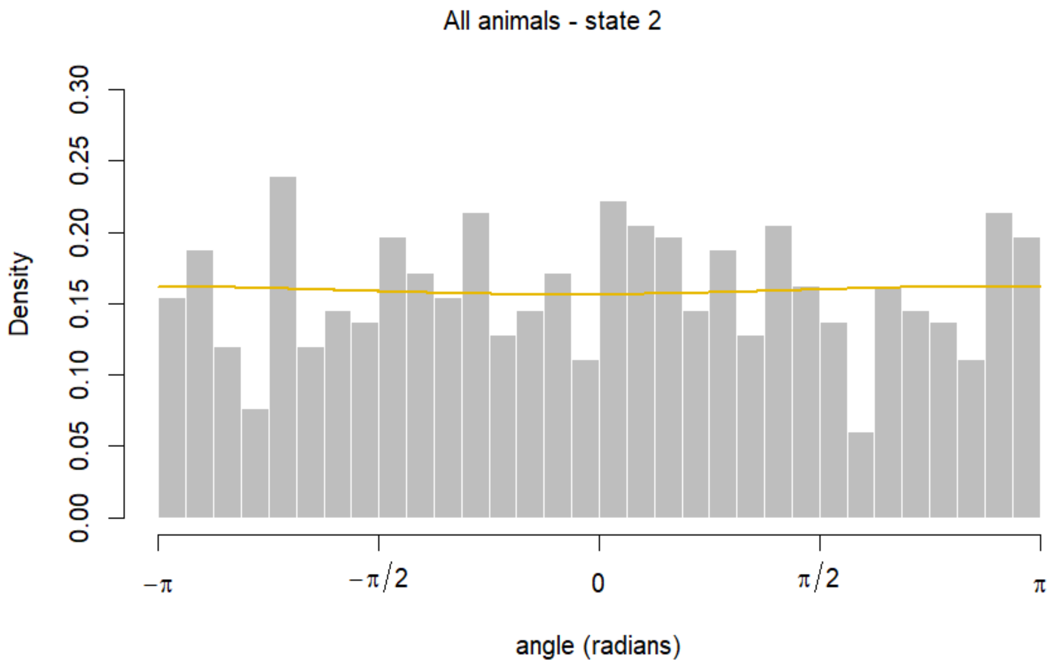
Supplementary Fig 1. Step length (km) distribution for state 1 (resting).



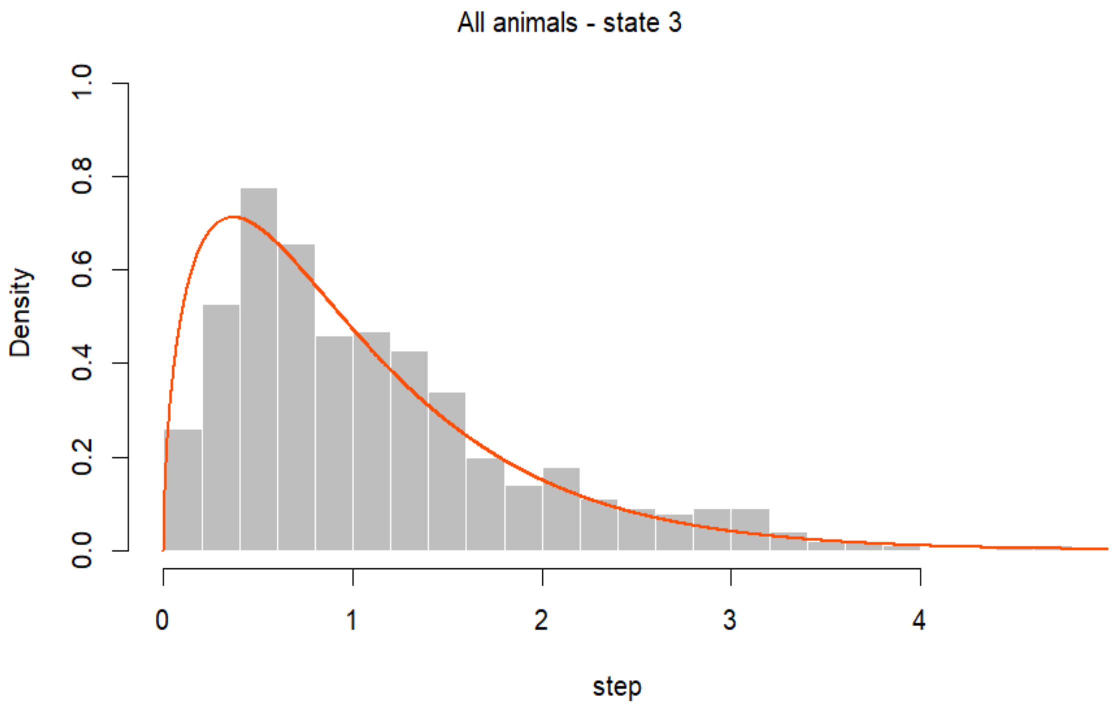
Supplementary Fig 2. Turning angle distribution for state 1 (resting)



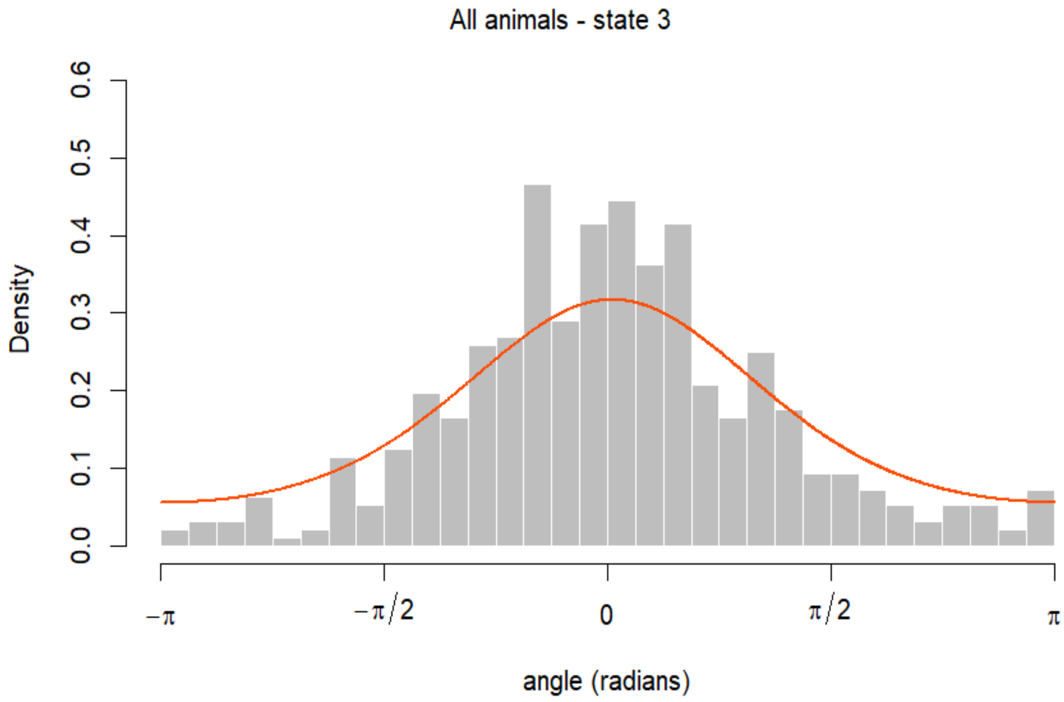
Supplementary Fig 3. Step length (km) distribution for state 2 (foraging).



Supplementary Fig 4. Turning angle distribution for state 2 (foraging)



Supplementary Fig 5. Step length (km) distribution for state 3 (traveling).



Supplementary Fig 6. Turning angle distribution for state 3 (traveling)

Supplementary Table 1: Number of guanaco years and GPS points per season for each individual.

ID	**Number of Guanaco Years**	**Number of GPS points in the spring-summer season**	**Number of GPS points in the autumn-winter seasons**
G01	1	1,443	1,458
G02	1	1,614	1,553
G03	1	573	493
G04	3	3,520	3,231
G05	3	4,976	4,472
G06	3	3,724	3,804
G08	1	914	831
G10	3	4,313	3,946
G11	1	1,614	1,623
G12	1	1,548	1,447
G13	1	1,460	1,496
G14	3	4,282	4,359
G15	1	1,633	784
G16	3	3,938	2,912
G17	2	3,016	2,437
G18	1	1,493	655
G19	2	2,171	2,469
G20	3	4,411	4,393
G21	1	570	841
G22	3	4,414	2,804
G24	3	3,971	4,316
G25	3	3,784	4,078
G26	3	5,185	4,742
G27	2	2,334	2,844

G28	1	1,544	1,494
G30	1	1,584	1,117
G32	1	371	1,481
G33	2	2,907	2,291
G34	1	2,391	3,062

Supplementary Table 2: Results of Akaike Information Criterion (AIC) model selection among a suite of models to determine variable inclusion. Variables included in the model selection process were Normalized Difference Vegetation Index from Landsat 8 satellites (NDVI), TRI (terrain ruggedness index), crossing covariate for the highway (Highway Crossing) and unpaved roads (Unpaved Crossing), distance to the highway (Distance to Highway) and unpaved roads (Distance to Unpaved Road), step length (sl), log of the step length (log_sl), and cosine of the turning angle (cos_ta). We also considered a quadratic relationship for NDVI. **Bolded models indicate that the inclusion of the proximity and crossing covariates, as well as a quadratic term for NDVI, improved the AIC score in comparison to models with only environmental and movement variables.**

AIC	**Covariates**
800762.2	**NDVI^2 + TRI + Highway Crossing + Unpaved Crossing + sl + log_sl + cos_ta**
800771.1	NDVI + TRI + Highway Crossing + Unpaved Crossing + sl + log_sl + cos_ta
801792.2	**NDVI^2 + TRI + Distance to Highway + Distance to Unpaved Road + sl + log_sl + cos_ta**
801799.3	NDVI + TRI + Distance to Highway + Distance to Unpaved Road + sl + log_sl + cos_ta
801802.0	NDVI^2 + TRI + sl + log_sl + cos_ta
801804.5	NDVI + TRI + sl + log_sl + cos_ta
802051.0	NDVI + sl + log_sl + cos_ta
802225.9	TRI + sl + log_sl + cos_ta

Supplementary Table 3: Continuous Boyce Index values for each model.

Model	**Continuous Boyce Index Value**
Proximity: Resting State: Summer	0.87
Proximity: Foraging State: Summer	0.84
Proximity: Traveling State: Summer	0.70
Proximity: Resting State: Winter	0.86
Proximity: Foraging State: Winter	0.71
Proximity: Traveling State: Winter	0.90
Crossing: Foraging State: Summer	0.97
Crossing: Traveling State: Summer	0.70
Crossing: Foraging State: Winter	0.71
Crossing: Traveling State: Winter	0.88

Chapter 4. Pumas and Penguins: a Novel Marine Subsidy Reshapes the Ecology of a Recovering Predator

ABSTRACT

Efforts to restore wildlife populations are increasing worldwide, yet many of these initiatives take place amidst significant ecological change. Wildlife are returning to novel ecosystems with transformed landscapes and new species compositions, leading to changes in behavior and interactions among species. In Patagonia, it is hypothesized that local extirpation of terrestrial predators, including the puma (*Puma concolor*), have facilitated the expansion of Magellanic penguin (*Spheniscus magellanicus*) colonies along Argentina's Atlantic coast. Recent wildlife conservation efforts fostering the recovery of puma populations in the area have resulted in a novel predator-prey relationship between pumas and penguins. Here, we integrate GPS collar and camera trap data to test how access to penguins, a novel marine resource, impacts puma behavior and population dynamics at Monte León National Park (MLNP). Based on the resource dispersion hypothesis, we expected pumas to adapt to this abundant resource in three key ways: 1) pumas that predate penguins would increase site fidelity and decrease their movement when penguins were present; 2) female pumas that predated penguins would have greater tolerance towards conspecifics; and 3) access to the penguin colony would lead to a high density of pumas. Our results showed that pumas that predated penguins significantly altered their movement patterns, including a higher degree of site fidelity to a single point source. This change in behavior has resulted in more frequent encounters among individual pumas, suggesting a greater tolerance for social interactions. Additionally, the penguin colony at MLNP now sustains the highest density of pumas recorded to date. The penguin colony at MLNP is shaping the outcomes of restoration for the park and driving the ecology of this recovering top predator.

INTRODUCTION

Wildlife restoration is increasingly used to combat biodiversity declines. A central objective of these efforts is to restore key trophic interactions that can shape ecosystems, including herbivory, predation, and scavenging (Bakker & Svenning, 2018; Cross et al., 2020; Ladouceur et al., 2022; Loch et al., 2020). The importance of restoring wildlife populations is reflected in ambitious conservation initiatives and international agreements, such as the Convention on Biological Diversity, the United Nations Environmental Programme, 30x30, and the UN Decade on Restoration (2021-2030) (Aronson et al., 2020; Maxwell et al., 2020; Tsioumani, 2020). Successful wildlife restoration efforts include scarlet macaws (*Ara macao*) in South America, tigers (*Panthera tigris)* in India, northern elephant seals (*Mirounga angustirostris*) along the Pacific coast of North America, and brown bears (*Ursus arctos*) and wolves (*Canis* *lupus*) in Europe (Bisht et al., 2019; Brightsmith et al., 2005; Cammen et al., 2019; Chapron et al., 2014).

Many wildlife restoration efforts occur against a backdrop of significant ecosystem changes that have occurred since the extirpation of the target species. Specifically, extensive anthropogenic and natural changes have fundamentally reshaped environments, resulting in the emergence of novel ecosystems characterized by altered habitats and distinct species compositions (Adeloff et al., 2015; Hobbs et al., 2009). For example, while the reintroduction of wolves is often justified by their ecological influence on prey populations and landscapes, recent studies in North America and Europe found limited impacts of recovered wolves on prey and primary producers (Hobbs et al. 2023; Kuijper et al. 2024). Hence, the outcomes of wildlife restoration in such novel ecosystems may be particularly difficult to assess as they can lead to new species behaviors and interactions (Kuijper et al., 2016, 2024; Valentine et al., 2020).

Due to their widespread influence on ecosystem structure and function, many wildlife restoration efforts have been centered on large carnivores. For predators, novel ecosystems could mean altered spatiotemporal distribution of resources (i.e. resource landscape), thus affecting when, where, and how animals obtain food, seek shelter, and acquire mates. In the Arctic, for instance, the decline in abundance of sea ice due to climate change has resulted in a decline of polar bear (*Ursus maritimus*) predation on ringed seals and an increase in predation on nesting seabirds and their eggs (Hamilton et al., 2017). To exploit dynamic and heterogeneous environments, carnivores must adapt their space use and movement patterns (Morales et al., 2010; Nathan, 2008). Yet, carnivore movement patterns might be constrained by territoriality and social tolerance of conspecifics (Gittleman, 2013). The Resource Dispersion Hypothesis can be used to predict the effect of a novel subsidy on consumer's behavior (Johnson et al., 2002). Specifically, it predicts that 1) carnivores will decrease space use as resources become less dispersed, and 2) multiple carnivores will use the same area to access resources when resources are abundant and costs (e.g. competition) are minimal (Johnson et al., 2002; MacDonald, 1983). The aggregation of multiple individuals may then lead to spatiotemporal changes in local and overall densities (Broekhuis et al., 2020). However, for carnivores, the effect of a novel subsidy may depend on their behavioral flexibility, which is typically thought to be lower than that of other taxa (Gittleman, 2013).

Here, we assess how access to the novel prey resource of Magellanic penguins, impacts puma behavior and density in coastal Patagonia. Following the European settlement of Patagonia during the 20th Century, pumas and several herbivores including guanacos (*Lama guanicoe*) and rheas (*Rhea pennants*) were largely extirpated to accommodate sheep ranching. The eradication of pumas and other mainland predators is hypothesized to have triggered the expansion of Magellanic penguin (*Spheniscus magellanicus*) colonies, formerly restricted to islands off the Atlantic coast of Argentina. More recently, conservation efforts have begun to establish protected areas to restore pre-settlement wildlife to Patagonia**.** The Monte León ranch on Argentina's coast, was home to a large breeding colony of Magellanic penguins (approximately 40,000 breeding pairs) (Millones et al., 2022). This ranch was donated to the Argentinean Park Service in 2004. Shortly after Monte León National Park (MLNP) was created, Magellanic penguin remains were found in puma scats, the first documentation of this interaction (Zanón Martínez et al., 2012). Despite predation by pumas, recent surveys conducted by the park have suggested that the penguin population is increasing, potentially indicating sustainability to this interaction (Millones et al. 2022). Still, beyond predation of penguins by pumas, little is known about how this novel interaction impacts puma behavior and population dynamics in the park.

The puma is the most widespread terrestrial carnivore in the Western Hemisphere (Hornocker & Negri, 2009; Karandikar et al., 2022; LaBarge et al., 2022). Pumas are generalist predators and have been found to consume as many as 232 different prey species as diverse as elk and porcupines (Karandikar et al., 2022). Additionally, pumas are considered to have a relatively fixed movement strategy, actively demarcating, and defending their boundaries against conspecifics (Hornocker & Negri, 2009). Like many other solitary carnivores, pumas are subject to regulation through density dependence and mutual avoidance through indirect signaling like scent marking and scraping (Hornocker & Negri, 2009). Generally speaking, females establish and defend home ranges that secure prey resources for both themselves and their kittens, while males establish and defend home ranges that provide access to multiple females. However, more recent research on pumas' behavior has found some flexibility in their social behavior (Elbroch et al., 2016, 2017; Elbroch & Quigley, 2017).

Magellanic penguins are abundant and distributed along the Atlantic Coast yet constrained to geographically small breeding colonies (Fig 1). In addition, Magellanic penguins are migratory and are only present at the park for about half the year (September - April). Based on the Resource Dispersion Hypothesis and puma ecology, we hypothesized that pumas will adapt to this spatially constrained and abundant resource in three ways: 1) pumas that predated penguins would increase their site fidelity, reduce movement, and aggregate at the penguin colony when penguins were present, 2) pumas, particularly female pumas, that predated penguins would increase their social tolerance of conspecifics to share the abundant resource, and 3) the penguin colony would lead to a high density of pumas in the park. To test these hypotheses, we first analyzed a dataset of GPS-collared pumas, assessing their movement patterns and social tolerance in the presence and absence of penguins (Abrahms et al., 2017). We then integrated GPS collar data and a camera trap array throughout the park to estimate puma density (Murphy et al., 2019). Our findings reveal that puma predation on penguins has surprisingly reshaped puma ecology. Pumas that predated penguins had drastically different movement patterns including increased site fidelity to a single point source. This behavior led to an increased encounter rate for individual pumas, indicating increased social tolerance. Finally, the penguin colony at MLNP supports the highest density of pumas ever recorded. This transformation of puma ecology at MLNP has important implications for understanding the ecological outcomes of rewilding along the Patagonian coast.

METHODS

Study Area

We conducted our fieldwork at MLNP, located in the Santa Cruz province of southern Argentina, from September 2019 to December 2023 (Figure 1). The park lies at an elevation of 0-350 meters above sea level and receives approximately 250 mm of precipitation annually. With a total area of 610 km^2, MLNP is characterized by a coastal steppe ecosystem comprising both shrubland and grassland habitats. The park is home to a substantial population of guanacos, rheas, and European hares, the typical prey species of pumas in the region (Walker & Novaro, 2010). Notably, the park contains 30 km of coastline, including a 2 km stretch that serves as a breeding colony for approximately 40,000 breeding pairs of Magellanic penguins (Millones et al., 2022).

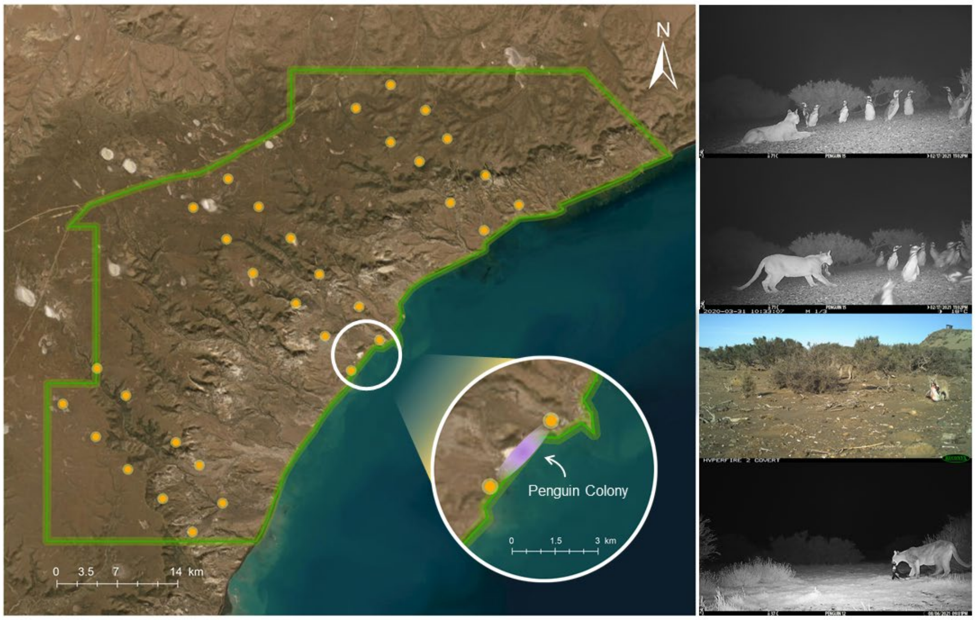


Fig 1. Camera trap grid at MLNP. The purple highlight in the inset map indicates the location of the single penguin colony in the park. Camera trap photos highlight photos of puma and penguin interactions caught on camera within the colony.

Monitoring puma movement

To monitor movement of puma in MLNP, we deployed GPS collars (Lotek Iridium Track M2D) on 14 adult pumas between September 2019 and December 2022, including 9 female pumas and 5 male pumas (supplementary table). All GPS collars were programmed to acquire location data at a 3-hour interval. Fieldwork was conducted on permit #DRPA 162 and subsequent renewals issued by Administración de Parques Nacionales (APN), Argentina.

Identifying Puma Diet

We classified individual puma diets as binary based on whether they predated penguins or didn't predate penguins. To distinguish between the pumas that predated penguins and the pumas that didn't, we investigated individual puma GPS clusters to identify prey items. We defined GPS clusters as any 2 or more points for the same puma within 20 m of each other over a 36-hour period (Smith et al., 2020). Field teams investigated a subset of clusters by conducting systematic searches to identify kill sites over a series of dedicated field seasons between September 2019 and January 2023. Clusters were investigated within 30 days of their first recorded locations. At investigated clusters, prey remains such as hair, skin, stomach contents, and bone fragments were used to identify the prey species. Based on confirmed penguin kills at clusters, pumas were subsequently classified as either pumas that predate penguins or pumas that don't predate penguins (supp table 1). GPS clusters are generally biased against detecting small prey like penguins (Bacon et al., 2011). Therefore, this methodology serves to identify pumas that have consumed penguins at least once, not to quantify the extent of their penguin predation.

Movement Metrics by Diet

We compared the movement patterns of individual pumas of different diets through seven movement metrics (Abrahms et al., 2017). We subset GPS data for individual pumas while penguins were present (October - April) and absent (June - August). We omitted the months of May and September, which were two months of transition when penguins were either arriving to breed or leaving to migrate. For each time period per individual, we used a subset of 3-months since the penguins are only completely absent from the park for a 3-month period. For individuals that were monitored for over a year, we treated each year of monitoring as separate individuals (referred to as a puma year) to account for changing behaviors between years of study. For each puma year and season, we measured 1) 95% kernel density home ranges, 2) mean step length (Euclidean distance from one relocation to the next), 3) mean turn angle correlation (the degree of similarity in directional changes from one relocation to the next), 4) mean residence time (the number of hours an individual spends inside a predefined radius over a predefined period of time), 5) mean time to return (the number of hours an individual spends before returning to a predefined radius), 6) mean volume of intersection (overlap between monthly 95% kernel density home ranges on a scale from 0 to 1), and 7) maximum net squared displacement (NSD, calculated as the maximum squared Euclidean displacement from the initial point in an animal's trajectory throughout its entire trajectory). Home range, mean step length, maximum net squared displacement, and mean turn angle correlation were calculated using the *amt* package. For mean residence time and mean time to return, the radius was set equal to 2x mean step length with a cut-off time of 12 hours (Abrahms et al., 2017). We used 12 hours to capture consecutive visits to the penguin colony. Mean residence time, mean time to return, and mean volume of intersection were calculated using *adehabitatLT* and *adehabitatHR*. Finally, we used linear mixed-effects models to compare variation in each movement metric with each group (Diet and Season) as a fixed effect and individual identity as a random effect. We then used least squares means and pairwise post-hoc comparisons to quantify differences between groups using the package *emmeans*.

To further test the site fidelity of pumas that predated penguins to the penguin colony, we calculated the number of returns to a previously visited area (i.e., revisitations) for each individual puma. We defined a revisit as a relocation within a radius of 2x the average step length of a previously visited location after the individual had left that location for over 12 hours (Abrahms et al., 2017). Again, we used 12 hours to capture consecutive visits to the penguin colony. All revisits were calculated using the *Recurse* package. We then used linear mixed-effects models to compare the variation in revisitations with distance to the penguin colony as a main effect and individual identity as a random effect for each season.

Puma Social Tolerance by diet

To examine puma social tolerance by diet, we defined puma interactions as simultaneous relocation data from any 2 individual pumas at a distance of less than or equal to 200m from each other. We used 200m as our threshold for consistency with previous studies looking at puma encounter rates (Elbroch & Wittmer, 2012). Individuals needed to separate from each other for greater than 12 hours before we counted another interaction. Again, we used a 12-hour threshold to account for daily visits, and therefore repeated encounters with conspecifics. Since each individual was monitored for different periods of time, we then calculated a weekly contact rate for each individual. We then fit a linear model with contact rate as the response variable and diet type as the fixed effect.

Next, we tested whether interactions occurred more frequently near the penguin colony using logistic regressions with a used vs. availability framework. We generated 10 random points for each puma interaction within the 95% kernel density estimation for all sampled pumas. We used the *lme4* package in R to run a univariate logistic regressions with the used and available points as the response variable and distance to the penguin colony as the fixed effect (Bates et al., 2015).

Estimation of puma density: Generalized Spatial Mark-Resight

In 2020, we established a camera trap grid of 32 cameras (RECONYX Hyperfire 2) spanning from the coast to the park border (Fig. 1). We used a clustered array design, with cameras spaced by 3km, to maintain spatial representation throughout the park while allowing for easier field implementation compared to regular spacing (Sun et al., 2014). We visited each camera approximately every 3 months to check the battery and download data. Each camera was set to take a burst of 3 photos when triggered. We sorted the photos of pumas by individual when they had GPS collars. All other photos of pumas were sorted as “unmarked”. We used the program *DigiKam* to tag all of the photos. Detections separated by more than 30 minutes from the next detection were considered to be independent (Ruprecht et al., 2021). The animal encounter data was split into 1-day occasions for the penguin-presence model from October 1st to December 31st, 2022, and 1-day occasions for the penguin-absence model from June 1st to August 31st, 2022.

To estimate the density of pumas in MLNP, we integrated a generalized spatial-mark resight model (gSMR) using both camera trap and GPS collar data (Ruprecht et al., 2021; Sollmann et al., 2013; Whittington et al., 2018). Generalized spatial-mark resight is a subset of spatial-mark resight models that can mitigate the bias introduced from the variation in camera detection rates for individuals that are marked. By including a submodel for the marking (i.e the GPS collaring of individual pumas) process, gSMRs are suitable when only a subset of the population is recognizable due to natural or artificial markings (here GPS collars). We incorporated GPS data from the marked individuals to inform the location of the activity center or collared individuals, the scale parameter in the detection function, and baseline detection rate. For each collared puma, we randomly selected 100 GPS locations to reduce temporal autocorrelation (Ruprecht et al., 2021).

We used Markov Chain Monte Carlo (MCMC) to draw samples from the posterior distributions for each parameter of interest. We used the R package 'NIMBLE' (de Valpine et al., 2017). For each model we ran three chains consisting of 50,000 iterations per chain and discarded the first 15,000 as burn in. We assessed model convergence by visually inspecting traceplots and ensuring the *Rhat* values were <1.1 (Gelman et al., 1996). For all parameters, we calculated the 95% highest posterior density intervals (HPDI) and the 95% Bayesian credible intervals (Chen & Shao, 1999).

RESULTS

Movement Metrics

Analysis of the movement metrics revealed differences by season and diet (Fig 3; least squared means and standard deviation in supplementary data). Pumas that predated penguins had more variable movement patterns between seasons. Specifically, individuals that predated penguins had significantly smaller home ranges, higher monthly mean volumetric intersection, a longer residence time, and a shorter time to return when penguins were present ($p < 0.05$ in all cases). In addition, pumas that predated penguins had a larger max NSD when the penguins were absent compared to all other groups ($p < 0.01$). In contrast, for individuals that did not predate penguins, there was no significant difference in each movement metric between seasons ($p > 0.05$). Further, there were no significant differences between diet or season for step length and turning angle ($p > 0.05$ in both cases; supplementary data).

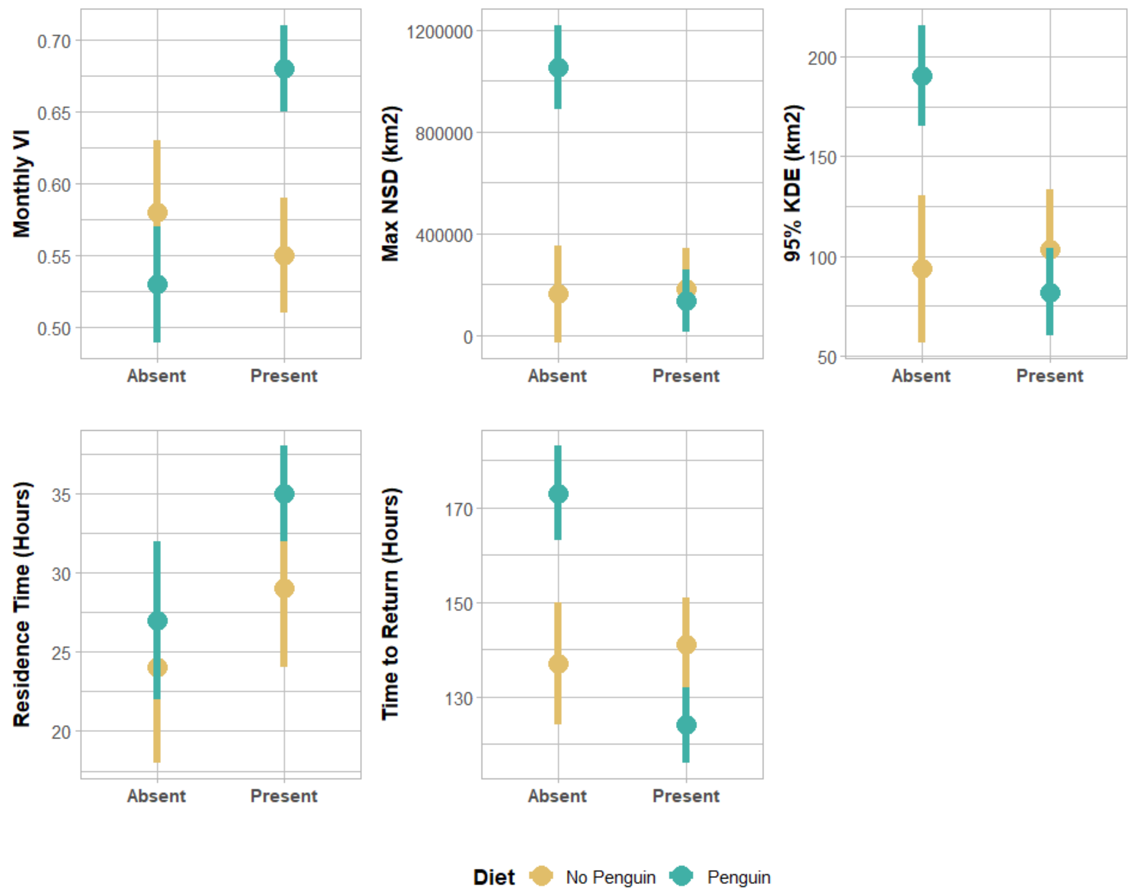


Fig 2. Means and standard deviations of the five puma movement metrics (monthly volumetric intersection, max net squared displacement, 95% kernel density home range, residence time, and time to return) with significant differences by diet (i.e. penguins vs. no penguins) and season (i.e. penguins absent vs. penguins present).

Site Fidelity

The analysis of revisitations suggested a high site fidelity to the penguin colony. Individuals that predated penguins had significantly more revisitations near the penguin colony both while penguins were present (estimate = -2.0e-3, 95% CI -3.0e-3 - -1.8e-3, $p < 0.01$) and absent (estimate = -5.3e-4, 95% CI -5.6e-4 - -5.0e-4, $p < 0.01$). In addition to a lower model coefficient estimate, the conditional R-squared value was slightly stronger while penguins were present ($R^2c = 0.51$) than when they were absent ($R^2c = 0.47$).

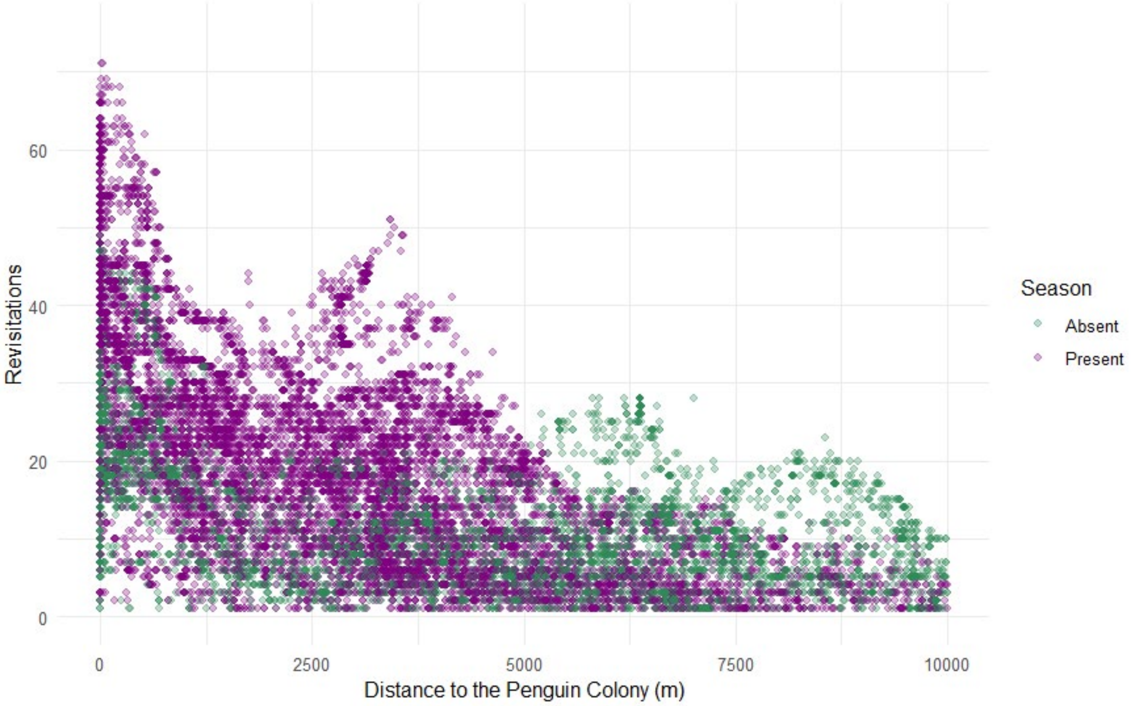


Fig 3. Number of puma revisitations across individuals that predated penguins by distance to the penguin colony separated by season (i.e. penguins absent vs. penguins present).

Social Interactions

We identified 295 puma-puma encounters from October 2019 to January 2023 between 14 individuals (supplementary data). There were 254 encounters between individuals that both predated penguins, 37 encounters between individuals with mixed diet types, and 4 encounters between pumas that did not predate penguins. Most encounters were between two females (n = 179), or between a male and female (n = 112). Only 4 encounters were between two males. Pumas that predated penguins had an average contact rate of 0.43 and pumas that did not predate penguins had an average contact rate of 0.09, nearly 5x higher (coefficient estimate = 0.33, 95% CI 0.12 - 0.54, $p < 0.01$). The majority of contacts were within 1km of the penguin colony (n = 185 or 63%) and were significantly more likely closer to the penguin colony (estimate = -2.4e-4, 95% CI -2.3e-4 - -1.8e-4, $p < 0.001$). Finally, of the contacts within 1km of the penguin colony, 131 (71%) were between two females.

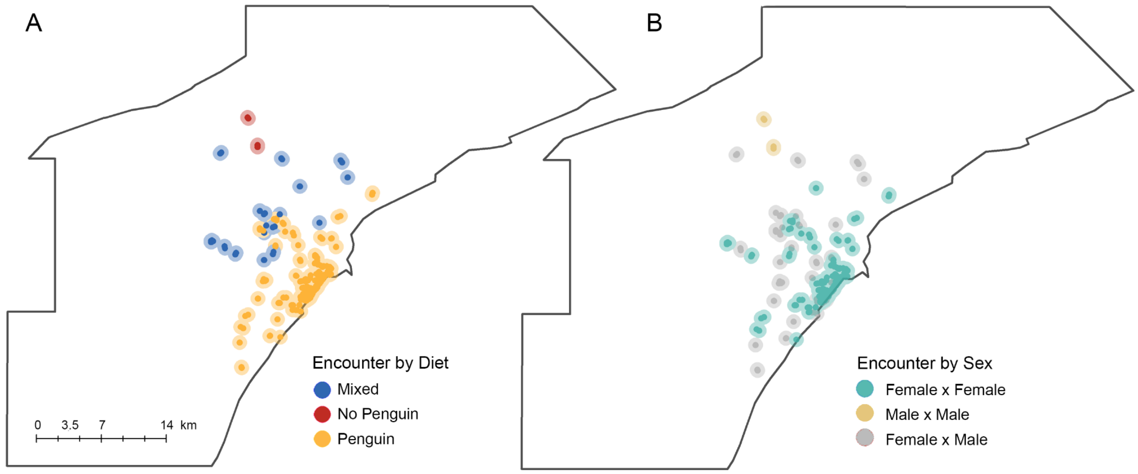


Fig 4. Locations of puma-puma encounters in MLNP. On the left (A), differences in colors represent the combined diet type of each individual. On the right (B), differences in colors represent the sex of each individual in a given encounter.

Puma Density Estimation

We obtained 110 independent photos of pumas (19 marked, 91 unmarked) in June - August while penguins were absent and 143 independent photos of pumas (29 marked, 114 unmarked) in October - December while penguins were present. The two camera traps closest to the penguin colony detected 54 (38%) independent photos of pumas when the penguins were present and 39 (35%) independent photos of pumas when the penguins were absent. Gelman-Rubin statistics (R-hat) for the density model were <1.1 for all parameters and visual inspections of trace plots indicated that the Markov chains successfully converged (supplementary data). While penguins were absent, puma density was estimated to be mean = 13.3 ± 2.2 individuals/km2 (95% CRI 8.6 - 16.1). Similarly, while penguins were present, puma density was estimated to be mean = 13.2 ± 2.3 individuals/km2 (95% CRI 8.4 - 16.6).

DISCUSSION

Wildlife restoration efforts are on the rise globally, but their ecological outcomes may be complicated by novel ecosystems. Here, we show how a novel interaction between pumas and penguins strongly shapes the behavior and abundance of a recovering apex predator. The puma exhibits extensive habitat flexibility, with its distribution spanning the majority of North and South America. Their expansive range encompasses a diverse array of habitats, from montane temperate regions to tropical ecosystems, and includes areas with varying degrees of anthropogenic disturbance. Our work shows that this flexibility extends to localized adaptation to a novel marine resource. In addition to the remarkable flexibility we observed in puma movement patterns and sociality, we documented the highest known puma population density. Further, these results illustrate how the restoration of a predator can lead to unexpected outcomes with the potential to cascade throughout this coastal Patagonian ecosystem.

Here, we find a clear example in which individual variation in movement by an apex predator is driven by a novel prey type. There is increasing evidence that movement patterns are much more flexible within populations than previously appreciated (Xu et al., 2021). Within-population variation, such as partial migration in ungulates or central-place foraging during breeding in seabirds, can be linked to seasonality, resource availability, or specific life stages (Xu et al., 2021). Orcas, for example, exhibit distinct movement patterns based on their target prey, forming residency and large social groups when preying on salmon, and displaying transient behavior and smaller social groups when targeting migratory pinnipeds (Beck et al., 2012; Ford et al., 1998). Our study reveals that pumas specializing on penguins adopt movement strategies closely resembling the characteristics of central-place foraging, indicated by high site fidelity (i.e., high residence time, shorter time to return, higher monthly volumetric intersection, and frequent revisitation of the penguin colony) (Abrahms et al., 2017). Pumas that prey on larger species, like guanacos, are already expected to have high residence times since larger prey can take multiple days to consume. Therefore, high residence time for pumas that predate penguins is particularly noteworthy and points to the high value of this resource for some individuals. When penguins are absent from the park, and marine resource availability declines, puma movement patterns shift dramatically. Home ranges significantly expand, and displacement distances increase, suggesting wider searches for food or territory. Interestingly, individuals still frequently revisit the colony when penguins are gone, possibly awaiting their return or scavenging penguin remains (personal communication with APN personnel). Penguins appear to be such an important resource, that once the penguins left MLNP, one individual puma left the park for another penguin colony 45 kilometers away. In general, the costs and benefits associated with different movement strategies for wildlife may change over time, continuously influenced by food availability, breeding opportunities, and predation risk. Our research suggests a deeper interplay between diet specialization and movement plasticity than previously appreciated, and in particular, that diet specialization on a novel resource can shape these patterns.

Historically, conspecific interactions were considered relatively rare for pumas, and restricted mainly to breeding behavior (Hornocker & Negri, 2009). However, we found a high rate of conspecific interactions at MNLP, with the penguin colony acting as a spatial anchor for these interactions. Specifically, compared to pumas that don't predate penguins, pumas specializing on penguins were nearly five times more likely to encounter conspecifics, primarily other females, in this resource-rich environment. These findings corroborate recent research that found higher overlap of puma territories in areas with higher prey density and the sharing of carcasses in resource poor environments (Elbroch et al., 2016, 2017; Elbroch & Quigley, 2017). Yet, in contrast to our findings, previous studies primarily found interactions in the form of direct reciprocity at kill sites between males and females (28), which seems unlikely in our case given the penguin's size and abundance (Elbroch et al., 2017). Instead, individuals, particularly females, appear to relax territoriality and increase their tolerance for each other near the colony. Without testing for genetic relatedness, we cannot rule out the Kinship Hypothesis, which suggests a fitness benefit for tolerating related individuals. Throughout the study period, we did observe numerous occasions in which mothers brought their kittens to forage in the penguin colony (Fig. 1). Still, given the numerous individuals that use the colony, it's unlikely that the Kinship Hypothesis can fully explain this phenomenon. Further, our collar data is sex biased towards females, so there may be other sex dynamics that we haven't fully captured. Elsewhere, there is increasing research that other supposed solitary carnivores, like jaguars, relax territoriality in environments with high prey densities (Eriksson et al., 2022). Collectively, this evidence highlights that sociality is more flexible and environment dependent than previously appreciated.

MLNP presents a unique case study of carnivore abundance driven by a novel resource. The intense space use and heightened tolerance for conspecifics observed near the colony, facilitate a population-level response, culminating in a density estimate far exceeding all previously reported density estimates according to a recent review of puma density (Murphy et al., 2022). Depending on specific methodological choices, density estimates can vary, and this review corrected density estimates that were not spatially explicit and/or included dependent individuals like kittens or juveniles (Murphy et al., 2022). Across these corrected densities, the 95th percentile for puma density was 3.7 independent pumas/100km2, and the highest documented density was in northeastern Argentina at 5.7 independent pumas/100km2 (Murphy et al., 2022; Rich et al., 2014). In other words, the density estimate for pumas at MLNP is nearly three times higher than the previously highest density estimate of pumas. Though increased site fidelity near the penguin colony could potentially inflate our density estimate, previous camera trap surveys within the colony further corroborate the observed phenomenon. In a previous study, we recorded 374 puma detections over 1800 camera trap nights (Serota et al., 2023). During that time, we recorded 5 different GPS collared pumas, however most of those detections (83%) were of uncollared pumas suggesting a high density within the colony.

This extraordinary high density likely arose from the penguin colony's concentrated abundant resources. Around the world, marine resources have led to hyperabundant populations of wolves, bears, jaguars, and coyotes (Eriksson et al., 2022; Roffler et al., 2022; Rose & Polis, 1998). When resources are concentrated at a single point source, like the penguin colony at MLNP, a high density of individuals is dependent on the benefit of sharing the resource outweighing the cost of defending it (MacDonald, 1983). Interestingly, this pattern then resembles grizzly bear populations that aggregate and tolerate multiple individuals at small streams with high densities of salmon. Historical evidence from the Pleistocene also suggests that coastal subsidies used to support terrestrial carnivore populations (Chamberlain et al., 2005). Taken together, it's possible that coastal environments around the world used to support high densities of terrestrial carnivores, but anthropogenic pressures and removal of carnivores in these systems have obfuscated our understanding of these dynamics (Doughty et al., 2016).

The restoration of wildlife to novel ecosystems presents unique challenges for conservation and management, and engenders questions about the ultimate objectives and philosophy of restoration efforts. Our study provides a compelling example, where the establishment of a protected area facilitated a novel predator-prey dynamic that led to unanticipated ecological outcomes. However, whether this is a desirable, undesirable, or neutral outcome is up for debate. Restoration goals, baselines, and benchmarks are often attributed to arbitrary points in time with incomplete ecological information (Jachowski et al., 2015; Sanderson, 2019). For novel ecosystems, how can management adapt a forward-looking approach with objectives that recognize the possibility, presence, and stability of novel interactions and their outcomes? At minimum, our research suggests managers and practitioners looking to restore wildlife populations should expect the unexpected.

SUPPLEMENTARY DATA

Supplementary Data SD1: Determination of diet for each individual puma. Individuals were classified under a "Penguin" diet if there was a documented instance of penguin predation.

Individual	Sex	Number of Clusters Investigated	Number and percentage of GPS points within 1km of penguin colony	# of confirmed penguin kills	Diet
P01	Male	76	0 (0%)	0	No Penguin
P02	Male	16	14 (6%)	2	Penguin
P03	Female	287	856 (33%)	32	Penguin
P04	Female	601	530 (26%)	39	Penguin
P05	Male	111	0 (0%)	0	No Penguin
P07	Female	198	317 (25%)	24	Penguin
P08	Female	203	227 (18%)	17	Penguin
P09	Female	177	281 (21%)	7	Penguin
P10	Male	59	0 (0%)	0	No Penguin
P11	Female	323	0 (0%)	0	No Penguin
P12	Female	383	0 (0%)	0	No Penguin
P13	Female	188	130 (20%)	1	Penguin

P14	Male	204	605 (25%)	9	Penguin
P16	Female	53	99 (17%)	2	Penguin

Supplementary Data SD2: Movement metrics for pumas when penguins are present vs. absent by diet type. Values are least-squares means ± SE. Within a row, least-squares means without a common superscript differ ($P < 0.05$)

Variable	**Diet: No Penguin**		**Diet: Penguin**	
	Absent	**Present**	**Absent**	**Present**
Step Length	847m ± 144m	956m ± 138m	805m ± 117m	912m ± 108m
Turning Angle Correlation	0.08 ± 0.04	0.01 ± 0.04	-0.02 ± 0.04	0.01 ± 0.03
95% KDE	93.7km2 ± 36.7km2^{ab}	103.6km2 ± 30.0km2^{ab}	190.3km2 ± 25.3km2^{a}	82.1km2 ± 21.7km2^{bc}
Monthly Volumetric Intersection	0.58 ± 0.05^{ab}	0.55 ± 0.04^{ab}	0.53 ± 0.04^{a}	0.68 ± 0.03^{bc}
Max NSD	163,463m ± 189,529m^{a}	185,152m ± 160,306m^{a}	1,053,231m ± 166,314m^{b}	137,076m ± 123,124m^{a}
Residence Time	24.0 hours ± 6.1 hours^{ab}	29.0 hours ± 5.1 hours^{ab}	26.5 hours ± 4.7 hours^{a}	35.4 hours ± 3.8 hours^{bc}
Time to Return	137 hours ± 12.6 hours^{ab}	141 hours ± 10.1 hours^{ab}	173 hours ± 10.1 hours^{a}	124 hours ± 7.5 hours^{bc}

Supplementary Data SD3: Puma encounter rates per individual.

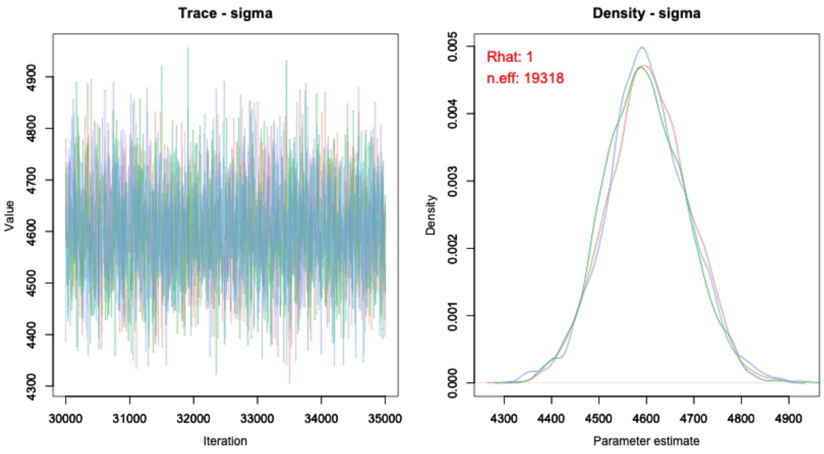
ID	Diet	Days Monitored	Weeks	Total Interactions	Contact Rate (Weekly)
P01	No Penguin	151	22	4	0.18
P02	Penguin	127	18	7	0.39
P03	Penguin	670	95	53	0.56
P04	Penguin	671	95	46	0.48
P05	No Penguin	495	70	9	0.13
P07	Penguin	371	53	32	0.60
P08	Penguin	405	57	43	0.75
P09	Penguin	588	84	35	0.42
P10	No Penguin	75	10	1	0.10
P11	No Penguin	840	120	8	0.06
P12	No Penguin	670	95	0	0
P13	Penguin	761	108	14	0.13
P14	Penguin	669	95	38	0.40
P16	Penguin	304	43	5	0.12

Supplementary Data SD4: Detection parameters for the generalized spatial mark-resight model estimating puma density. σ = scale parameter, $\lambda 0_{resight}$ = baseline detection rate for camera analyses, and $\lambda 0_{marking}$ = baseline detection rate for the marking process.

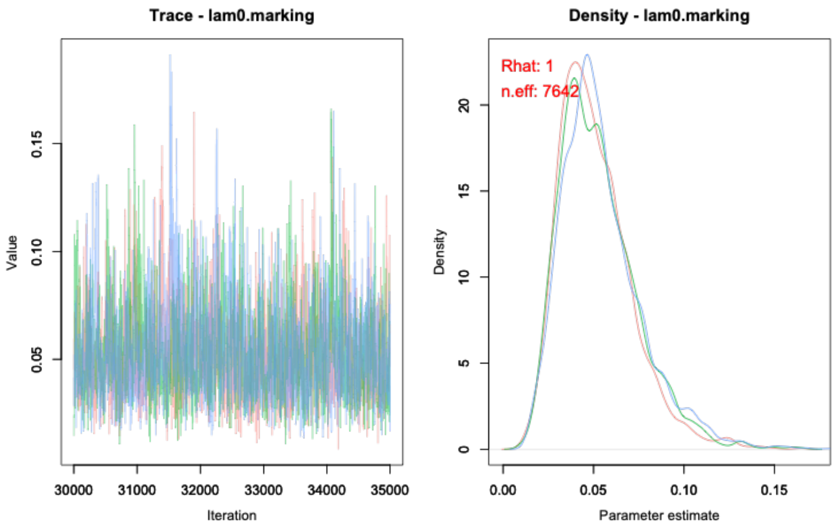
Parameter	Mean (SD)	2.5% CI	50% CI	97.5% CI	R-hat
Penguin Presence					
Density (per 100 km^2)	13.3 (2.2)	8.6	13.5	16.1	1.00

σ	4599 (87)	4433	4597	4772	1.00
$\lambda 0_{resight}$	.002 (.0004)	0.001	0.002	0.003	1.01
$\lambda 0_{marking}$	0.05 (0.02)	0.02	0.05	0.10	1.00
Penguin Absence					
Density (per 100 km^2)	13.2 (2.3)	8.4	13.5	16.6	1.00
σ	4598 (86)	4434	4597	4773	1.00
$\lambda 0_{resight}$	0.002 (0.001)	0.001	0.002	0.003	1.00
$\lambda 0_{marking}$	0.05 (0.02)	0.02	0.05	0.10	1.00

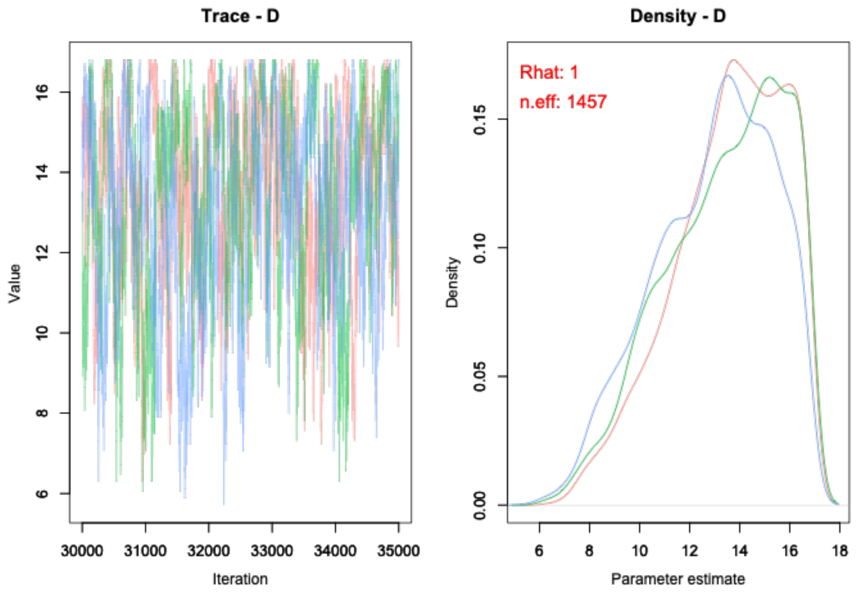
Supplementary Data SD5: Trace plot and estimate for the spatial scale parameter (σ) of pumas with R-hat and effective sample size for all three chains (represented as different colors) for the penguin presence gSMR model.



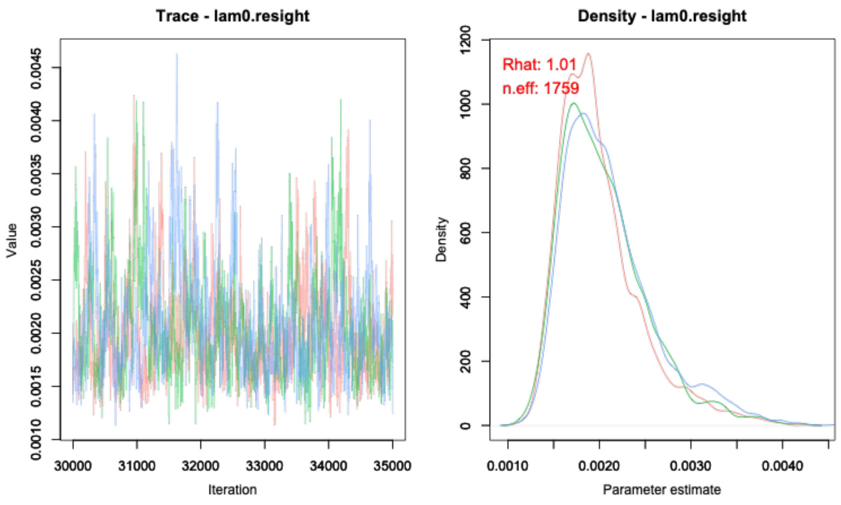
Supplementary Data SD6: Trace plot and estimate for the baseline puma detection rate for the marking process ($\lambda 0_{marking}$) with R-hat and effective sample size for all three chains (represented as different colors) for the penguin presence gSMR model.



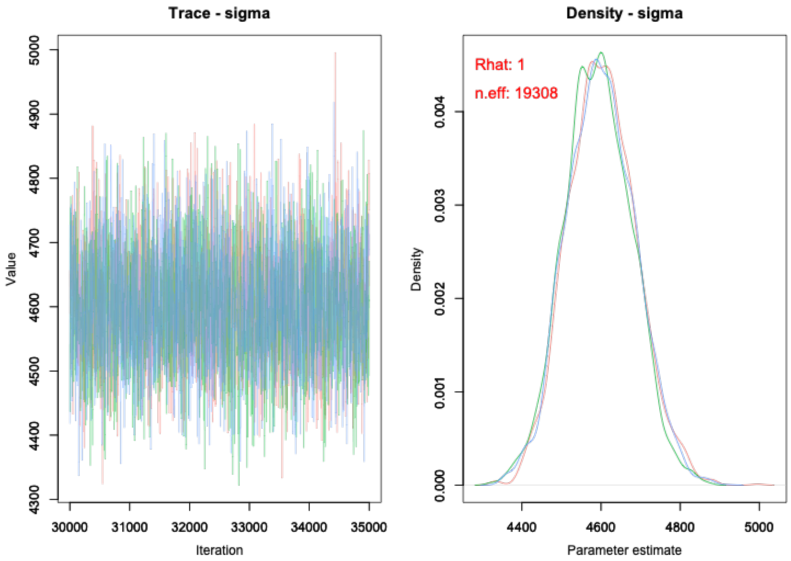
Supplementary Data SD7: Trace plot and estimate for puma density (D) with R-hat and effective sample size for all three chains (represented as different colors) for the penguin presence gSMR model.



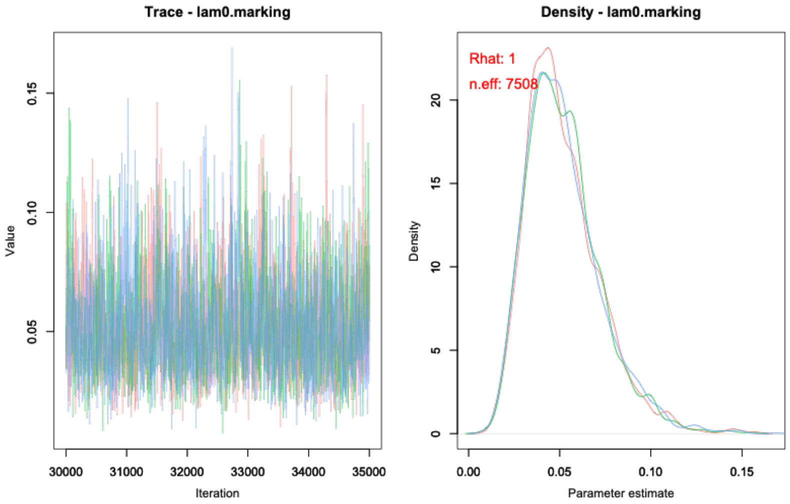
Supplementary Data SD8: Trace plot and estimate for the baseline puma detection rate for the camera analysis ($\lambda 0_{resight}$) with R-hat and effective sample size for all three chains (represented as different colors) for the penguin presence gSMR model.



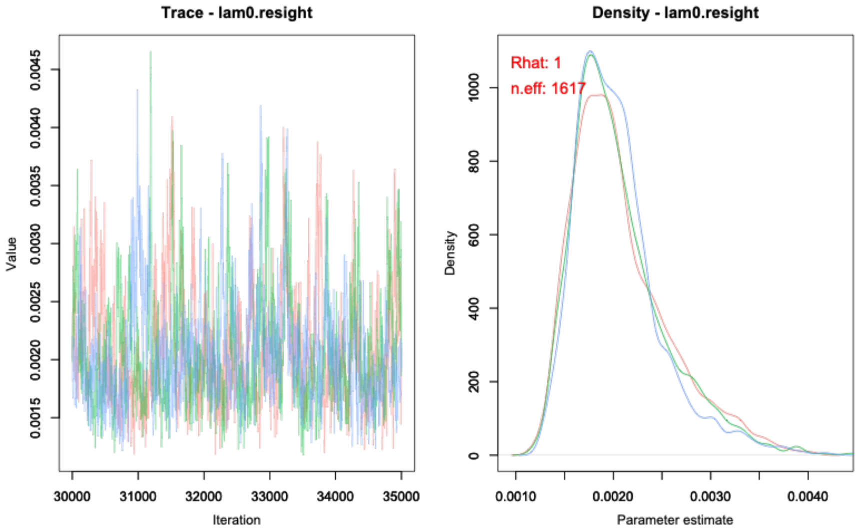
Supplementary Data SD9: Trace plot and estimate for the spatial scale parameter (σ) of pumas with R-hat and effective sample size for all three chains (represented as different colors) for the penguin absence gSMR model.



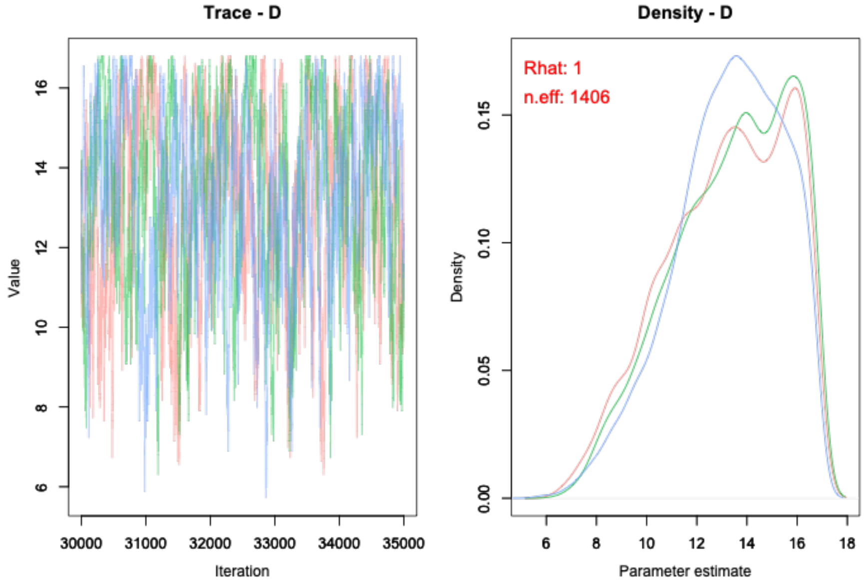
Supplementary Data SD10: Trace plot and estimate for the baseline detection rate of pumas for the marking process ($\lambda 0_{marking}$) with R-hat and effective sample size for all three chains (represented as different colors) for the penguin absence gSMR model.



Supplementary Data SD11: Trace plot and estimate for the baseline detection rate of pumas for the camera analysis ($\lambda 0_{resight}$) with R-hat and effective sample size for all three chains (represented as different colors) for the penguin absence gSMR model.



Supplementary Data SD12: Trace plot and estimate for puma density (D) with R-hat and effective sample size for all three chains (represented as different colors) for the penguin absence gSMR model.



Chapter 5. A Marine Subsidy Shifts Puma Predation Patterns on a Large Terrestrial Herbivore

ABSTRACT

The restoration of top predators is often sold on its ability to reestablish lost predator-prey dynamics and improve ecosystem structure and function. However, novel environments can shift the distribution of prey for predators and influence their foraging strategies. In general, either the *Prey Abundance Hypothesis* or the *Prey Catchability Hypothesis* can help explain the predation patterns for predators. In multi-prey systems, predators may need to adjust their behavior to switch between prey, potentially obfuscating predation patterns. At Monte León National Park (MLNP), pumas have adapted to predating penguins, a novel and abundant resource. This has led to a spatial aggregation and high density of pumas near a geographically small penguin colony. However, it's unclear how this change in behavior and density impacts guanacos, the primary prey for pumas throughout the region. Using GPS collar and predation data from a puma-guanaco-penguin system, we tested how this seasonally-abundant novel prey impacted predation risk for guanacos. We found that the probability of an encounter between pumas and guanacos was driven by the penguin colony, whether the penguins were present or absent. However, proximity to the penguin colony only increased the probability that a puma captured a guanaco when penguins were absent. This seasonal decoupling of encounter and capture probability suggests that pumas might become satiated when penguins are present at MLNP, resulting in a reduced predation risk near the colony. Our results highlight how novel ecosystems can alter predator-prey dynamics and lead to unexpected restoration outcomes.

INTRODUCTION

Around the world, large-scale conservation efforts have led to the recovery of top predators, like brown bears (*Ursus arctos*) in Europe and leopards (*Panthera pardus*) in India (Athreya et al., 2013; Chapron et al., 2014; Perino et al., 2019; Stier et al., 2016). These efforts often aim to restore lost or altered predator-prey interactions, which play a crucial role in shaping ecosystems (Bakker & Svenning, 2018; Cross et al., 2020; Perino et al., 2019). Predator-prey interactions can have profound impacts on ecosystem structure and function by regulating population dynamics, driving nutrient transport and deposition, and influencing prey behavior (Estes et al., 2011; Monk & Schmitz, 2022; Schmitz et al., 1997). However, human influences like climate change, land-use change, and the introduction of invasive species are increasingly disrupting predator-prey interactions (Guiden et al., 2019; Kuijper et al., 2016, 2024). These altered ecological conditions can affect animal behaviors, distributions, and abundances, subsequently influencing the spatiotemporal dynamics of predator-prey interactions (Kuijper et al., 2016; Van Scoyoc et al., 2023). For example, in urbanized environments pumas (*Puma concolor*) are quick to abandon their kills to avoid encounters with humans, causing them to increase predation rates on deer (*Odocoileus hemionus*). Similarly, invasive predators go undetected by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) (Kuehne & Olden, 2012). Therefore, we need to understand how predator-prey interactions are shifting in novel environments to fully grasp the downstream ecological consequences of anthropogenic effects.

Alterations to ecosystems can shift the distribution of resources thereby impacting foraging strategies for predators (Guiden et al., 2019). The predation patterns for predators looking to maximize resource acquisition in heterogeneous landscapes can be explained by either the *Prey Abundance Hypothesis* or the *Prey Catchability Hypothesis* (Balme et al., 2007; Hopcraft et al., 2005; Smith et al., 2020). The *Prey Abundance Hypothesis* posits that predation patterns mirror local prey distribution with increased predation in areas with higher prey abundance (Balme et al., 2007; Hopcraft et al., 2005; Smith et al., 2020). Conversely, the *Prey Catchability Hypothesis* suggests that spatial patterns of predation will align with capture probability upon encounter, reflecting predator preference for habitats that enhance prey capture success (Balme et al., 2007; Davidson et al., 2012; Hopcraft et al., 2005; Smith et al., 2020).

However, multi-prey systems can complicate the tradeoffs between prey abundance and catchability of primary prey if predators behaviorally adapt and switch to alternative prey (Brunet et al., 2023; Kjellander & Nordström, 2003; Montgomery et al., 2019; Wittmer et al., 2014). If both prey species' space use overlaps, predators may be able to exploit each prey type without altering their habitat use (Brunet et al., 2023). Still, even when multiple prey overlap, encountering a predator may not be risky if predators prefer one prey type over another or are already satiated (Suraci et al. 2022). Conversely, if the distribution or catchability of each prey species varies, predators may need to shift their space use to facilitate prey switching and favor encounters and catchability of one species over the other. In some cases, prey switching can lead to apparent competition (Holt, 1977). Apparent competition is widely recognized as a leading mechanism for the decline of some species of conservation concern (Holt & Bonsall, 2017; Wittmer et al., 2013). For example, in British Columbia, increased mortality of the threatened boreal caribou (*Rangifer tarandus caribou*) is thought to have been triggered by increases in the moose (*Alces alces*) population and subsequent increase in wolf densities (Wittmer et al., 2007). Therefore, identifying predator spatial tradeoffs to exploit primary and alternative prey and their effects can play a critical role in conservation.

The puma is the most widespread terrestrial carnivore in the Western Hemisphere (Iriarte et al., 1990). Pumas are broadly considered to be generalist predators who readily exhibit prey switching behavior and consume as many as 232 different prey items across their range (Karandikar et al., 2022). As ambush predators, pumas actively seek habitat with dense tree or shrub cover and rugged terrain to stalk their prey (Coon et al., 2020; Elbroch & Wittmer, 2012; Hornocker & Negri, 2009; Smith et al., 2020). Across the Patagonian steppe, guanacos (*Lama guanicoe*) are the primary prey for pumas, and puma predation of guanacos has been the only large predator-prey dynamic in the region for nearly 10,000 years (Donadio et al., 2022). Following European colonization in the late 19th century, sheep ranching became the dominant economic activity. This led to declines in both puma and guanaco abundance and distribution across the steppe (Walker

& Novaro, 2010). To combat the decline in puma and guanaco populations, large-scale wildlife restoration and conservation initiatives began purchasing old ranches and converting them to parks. Efforts like these have led to the recovery of some puma and guanaco populations (Walker & Novaro, 2010).

Monte León National Park, established in 2004 after the purchase of a coastal ranch, is home to abundant populations of both pumas and guanacos (Walker & Novaro, 2010). The park also supports a large colony of 40,000 Magellanic penguin (*Spheniscus maggellanicus*) breeding pairs (Millones et al., 2022). The extirpation of pumas in the late 19th century is hypothesized to have allowed the colonization of Magellanic penguin colonies along the Argentina coast (Borboroglu & Boersma, 2013; Cruz et al., 2014). Shortly after the park was established, puma predation of penguins was documented for the first time (Zanón Martínez et al., 2012). Due to this abundant and easily catchable marine resource, Monte León National Park has become a novel, multi-prey ecosystem for pumas. This, in turn, has led to the park boasting the highest reported puma density in the world (Chapter 3). In addition, previous research has shown that pumas in the park aggregate at high densities near the penguin colony, a 2 km stretch of beach (Chapter 3). Even when the penguins migrate away from the park in the winter, pumas still aggregate near the penguin colony (Chapter 3). Notably, penguin predation is seasonal, occurring only during the penguins' onshore breeding period (September - April).

To improve our understanding of how the risk of predation for primary prey is altered by a seasonally-abundant novel alternative prey, we tested four alternative hypotheses in a puma-guanaco-penguin system in southern Patagonia (Table 1). We hypothesized four possible predation patterns in Monte León: 1) that the penguin colony increases predation risk for primary prey (guanacos) by attracting a high density of predators; 2) that the penguin colony decreases predation risk for primary prey by providing an abundant and accessible alternative source of food; or 3) that the penguin colony alternately decreases and increases predation risk for primary prey by season, with puma predation risk decreasing for guanacos when penguins are present and increasing when penguins are absent. Our fourth potential hypothesis is that the penguin colony has no effect on predation risk for primary prey. This may occur if a) pumas that target penguins target other alternative prey when penguins are absent, b) landscape features, other than proximity to the penguin colony, determine where guanacos are killed or c) guanaco abundance best predicts guanaco kill locations. To test these hypothese and identify the mechanisms underlying variation in predation risk, we used GPS data from tagged pumas and guanacos to evaluate changes in encounter probability (i.e., spatiotemporal overlap between pumas and guanacos) and capture probability (i.e., guanaco kill site selection by pumas) (Table 1).

Table 1. Hypotheses and predictions for how the risk of predation for primary prey (guanacos) is impacted by alternative prey (penguins).

Alternative Hypothesis	**Prediction**
1. The penguin colony increases predation risk for primary prey	Capture probability and encounter probability increases near the penguin

(guanacos) by attracting a high density of predators.	colony when penguins are both present and absent.
2. The penguin colony decreases predation risk for primary prey by providing a readily available and abundant source of food.	Capture probability decreases near the penguin colony when penguins are both present and absent.
3. The penguin colony alternately decreases and increases predation risk for primary prey by season; predation risk for primary prey decreases when the alternative prey are present and predators are satiated and increases when they're absent.	Encounter probability increases near the penguin colony when penguins are both absent and present, but capture probability only increases when penguins are absent.
4. The penguin colony has no effect on predation risk for primary prey, because a) predators that target penguins target other alternative prey when penguins are absent, b) landscape features primarily determine where predators kill prey (*Prey Catchability Hypothesis*), or c) the presence and abundance of primary prey primarily determines where predators kill prey (*Prey Abundance Hypothesis*).	a) Pumas that predate penguins don't predate larger prey when penguins are present or absent. b) *Prey Catchability Hypothesis*: Habitat features that facilitate stalking and ambush tactics (forage cover, steeper slopes, and ruggedness) drive capture probability when penguins are both absent and present (Balme et al., 2007; Cristescu et al., 2019; Smith et al., 2020). c) *Prey Abundance Hypothesis*: Both encounter and capture probability increase with increasing distance from the penguin colony, as previous research on guanaco habitat use from MLNP has shown that guanacos select for the traditional steppe habitat and roads further away from the colony (Chapter 2; Verta, 2022).

METHODS

Study area

Monte Leon National Park, established in 2004, is situated on the eastern Argentine coast within the Santa Cruz province. Encompassing 61,000 hectares, the park is characterized by a coastal steppe ecosystem featuring shrubland and grasslands (Oliva et al., 2006). Dominant plant species in the shrublands include black shrub (*Mulguraea tridens*) and pince-scented daisy (*Lepidophyllum cupressiforme*), while the grasslands are dominated by thatching grass (*Festuca pallescens*), salt grass (*Puccinellia sp.*), bentgrass (*Agrostis sp.*), and coast tussock-grass (*Poa atropidiformis*). Average annual precipitation is 255 mm, characterized by rainfall during the autumn-winter months (April-September) and a dry season in spring-summer (October-March) (Paruelo et al. 1998). Average temperatures are 4.7 °C during autumn-winter and 13.8 °C during spring-summer. The park is home to a population of guanacos, rheas, and European hares, the typical prey species of pumas in the region (Walker & Novaro, 2010). Notably, the park contains 30 km of coastline, including a 2 km stretch that serves as a breeding colony for approximately 40,000 breeding pairs of Magellanic penguins (Millones et al., 2022) (Figure 1). While there is variation in the timing of arrival and migration, penguins are generally present within the park between September and April and absent from May through August (Borboroglu & Boersma, 2013).

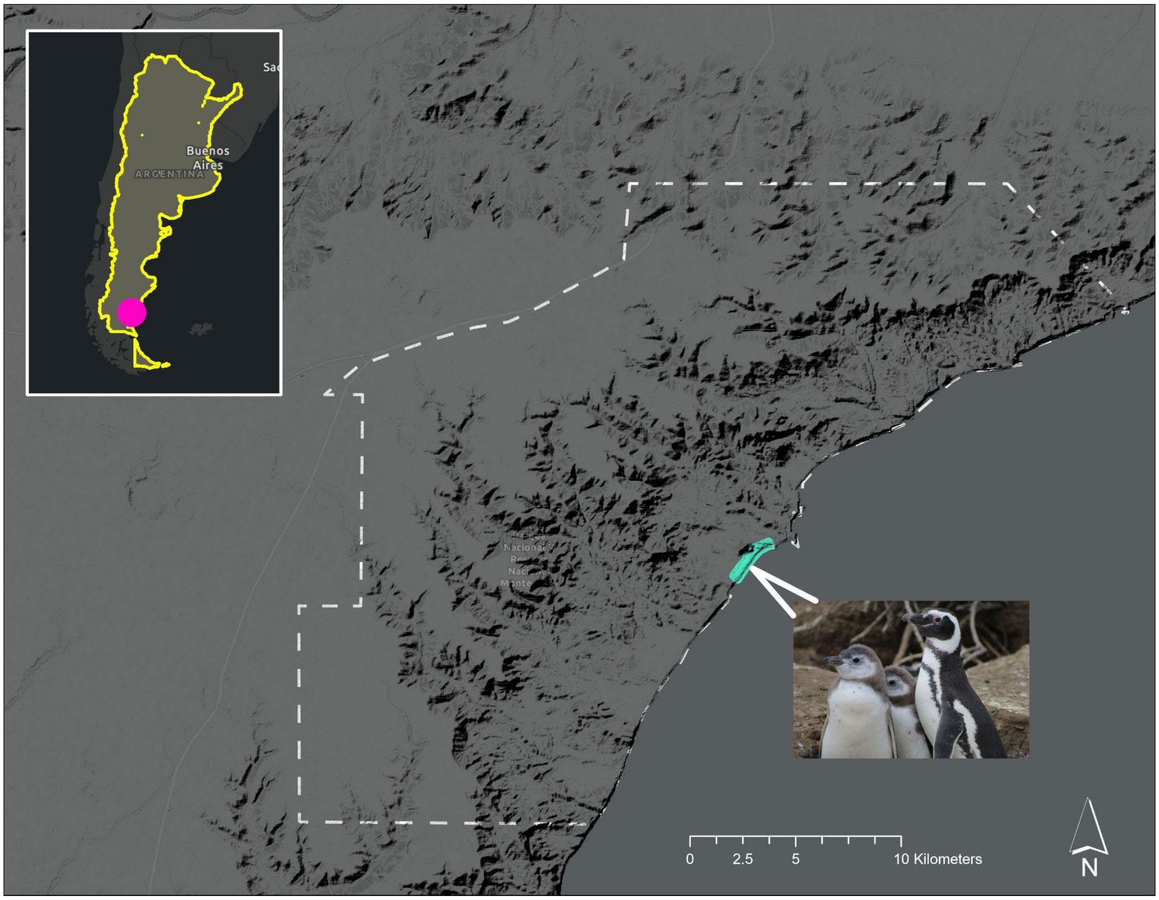


Fig 1. Map of Monte Leon National Park, Santa Cruz, Argentina. Teal highlight and photo of Magellanic penguins indicate the location of the penguin colony. Inset map of Argentina with a pink dot representing the location of MLNP.

GPS collaring of pumas and guanacos

To monitor the movement of both pumas and guanacos in MLNP, we deployed GPS collars (Lotek Iridium Track M2D) on 14 adult pumas (9 females and 5 males) and 29 adult guanacos (14 males and 15 females) between September 2019 and December 2022. GPS collars were programmed to acquire location data at a 3-hour interval for pumas and 2-hour intervals for guanacos. Fieldwork and animal captures were conducted under permit IF-2019-111378017-APN-DRPA#APNAC and subsequent renewals issued from the National Park Administration of Argentina (Administración de Parques Nacionales), and UC Berkeley IACUC Protocol # AUP-2019-10-12628.

Environmental covariates

We used remotely sensed data to determine the Normalized Difference Vegetation Index (NDVI), Elevation, Slope, and Terrain Ruggedness Index (TRI) for each puma-guanaco encounter location and predicted kill site (see below). We calculated TRI (the mean of the absolute difference between the value of a cell and its 8 surrounding cells), slope, and elevation from NASA's ⅓ arc-second digital elevation model using the *Terra* package in Program R version 4.0.5 (R Core Team, 2021). For NDVI, we used the *rgee* and *reticulate* package in R to match each GPS location with the closest 30 m spatial resolution Landsat 8 image (every 16 days) and calculated the Normalized Difference Vegetation Index (Data available from U.S. Geological Survey). In addition to the remotely sensed data, we created a raster layer specifying the distance to the penguin colony at MLNP using the *Terra* package (Hijmans, 2023).

Predation Rate

To test for differences in predation rate by diet type and season, we used a kill site model developed by Karandikar (2023). We identified clusters of individual puma GPS points, defined as two or more consecutive GPS locations for the same individual puma located within 20 m of each other in a period of 36 hours, to investigate potential kill sites (Smith et al., 2020). Field teams investigated a subset of these clusters by conducting systematic searches to identify potential kill sites during dedicated field seasons between September 2019 and December 2022. To account for the spatial and temporal biases associated with investigating a subset of clusters, we then modeled kill site selection of large prey (guanacos and rheas) as a function of biological and ecological influences. Further details regarding specific model development choices can be found in Karandikar (2023).

We further subset the predicted kills dataset to better reflect the ecology of the system. First, we excluded from consideration all predicted kills within 500 m of the penguin colony to ensure we were estimating kill site selection for large prey specifically. Throughout the entirety of our study, neither field crews nor a large array of camera traps ever recorded a guancao or rhea carcass within 500 m of the colony. We therefore considered these clusters to be penguin kills. Second, to reduce pseudoreplication, if multiple clusters were within 200 m of each other in a period of 48 hours, we only kept the first cluster. Pumas can sometimes move their prey as far as 200 m over the course of the several days it takes to consume it and will also bed near the carcass (Bauer et al., 2005), resulting in multiple clusters for a single kill site. We calculated weekly predation rates of large prey per individual puma. To delineate by diet type, we used a binary classification of penguin eaters vs. non-penguin eaters based on evidence of penguin predation from our cluster dataset (see Chapter 3 for additional details). We then tested for differences between diet type (penguin eaters and non-penguin eaters) and season (penguin presence and penguin absence) by fitting a linear model with the weekly predation rate as the response variable and diet type, season, and an interaction between diet type and season and covariates.

Encounter probability

An encounter was defined as an event where a GPS collared guanaco and a GPS collared puma were simultaneously within 350 m of one another (Smith et al., 2020). Our encounter distance reflects a more conservative approach to predator-prey encounter modeling since pumas are ambush predators more effective at short striking distances (Courbin et al., 2016). To model encounter probability, we implemented a used vs. availability design where the used points were the GPS locations of encounters and the available points were 10 random points per encounter. We sampled the available points from the overlap of the combined 95% kernel density estimate of all sampled pumas and the 95% kernel density estimate of all sampled guanacos. We used an ad-hoc method to estimate the smoothing parameter in both cases (Calenge, 2006). To test how the penguin colony impacts the encounter probability, we estimated a logistic regression model with encounter (yes/no) as the response variable and elevation, slope, TRI, NDVI, and distance to the penguin colony as predictor variables. All covariates were scaled and centered. Slope was correlated with TRI (R = 0.98), and elevation was correlated with distance to the penguin colony (R = 0.51); correlated covariates were not considered in the same model. We ran a model for all possible combinations of covariates and ranked them using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; (Burnham & Anderson, 2002). Following Burnham and Anderson (2002), we considered models with ΔAIC_c 0-2 to have empirical support. When several competing models had a ΔAICc 0-2, we retained the most parsimonious model (Arnold, 2010). Finally, to assess the predictive performance of our top-ranked model, we used the continuous Boyce Index (Hirzel et al., 2006). The continuous Boyce Index is a presence-only metric ranging from -1 to 1, with values closer to 1 indicating greater model performance in predicting encounters.

Predation risk

To test how the penguin colony impacts predation risk across MLNP, we ran a mixed effects logistic regression model with used vs. available kill site locations as the response variable and we considered predictor variables that included elevation, slope, TRI, NDVI, and distance to the penguin colony. We included random slope effects for each individual. All covariates were scaled and centered. Again, slope was correlated with TRI (R = 0.98) and elevation was correlated with distance to the penguin colony (R = 0.51); these pairs were therefore not considered in the same model. We used a 10:1 ratio of used:available kill sites, which we sampled randomly within each puma's 95% home ranges (Smith et al., 2020). Home ranges were estimated from individual kernel utilization distributions with an ad hoc method to estimate the smoothing parameter (Calenge, 2006). Across all possible combinations of covariates, we examined support for each model that included at least one of our covariates. We selected models following the same procedure as for encounter probability.

RESULTS

Predation Rate

Overall, we identified 348 large prey predation events from 2,378 investigated clusters. We detected 200 predation events of large prey when the penguins were present (September - April) and 148 predation events of large prey when the penguins were absent (May - August). Weekly predation rates varied widely by diet type. Pumas that did not predate penguins had a higher predation rate of large prey, predating 0.71 large prey items weekly (0.72 while penguins were present and 0.79 while penguins were absent) compared to 0.35 large prey items weekly for pumas that predated penguins (0.26 while penguins were present and 0.44 while penguins were absent) (Supplementary Data SD1; Fig. 2). Our model also revealed a lower predation rate on large prey for pumas that predated penguins (diet type **β** = -0.35; 95% CI -0.57 - -0.12). Confidence intervals for season and the interaction between diet and season overlapped zero.

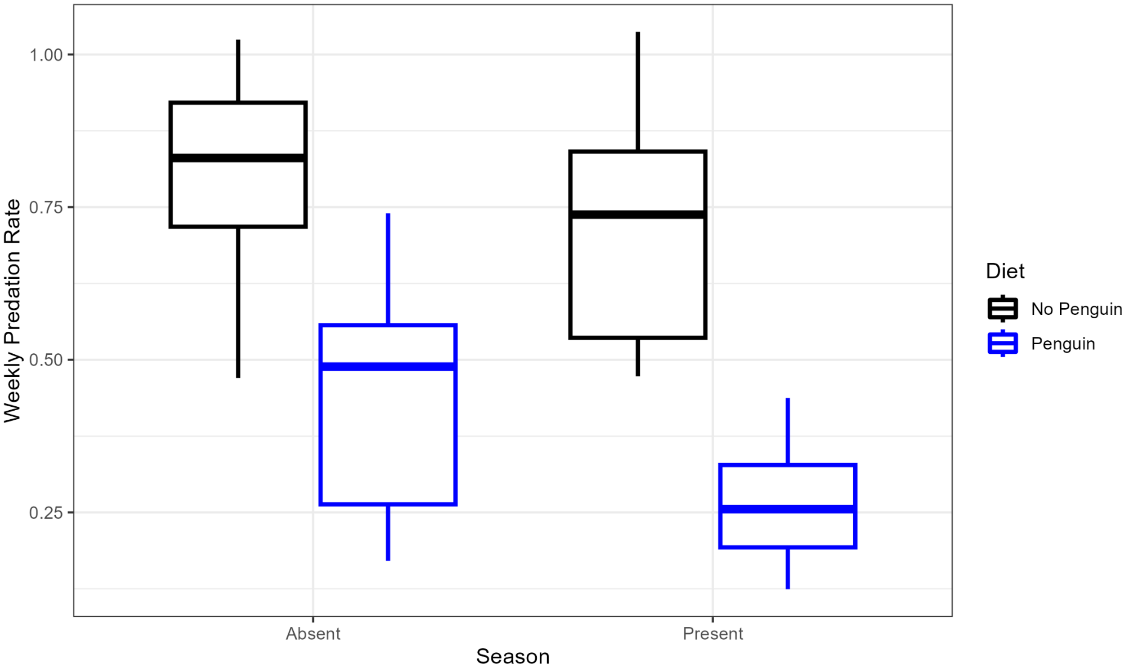
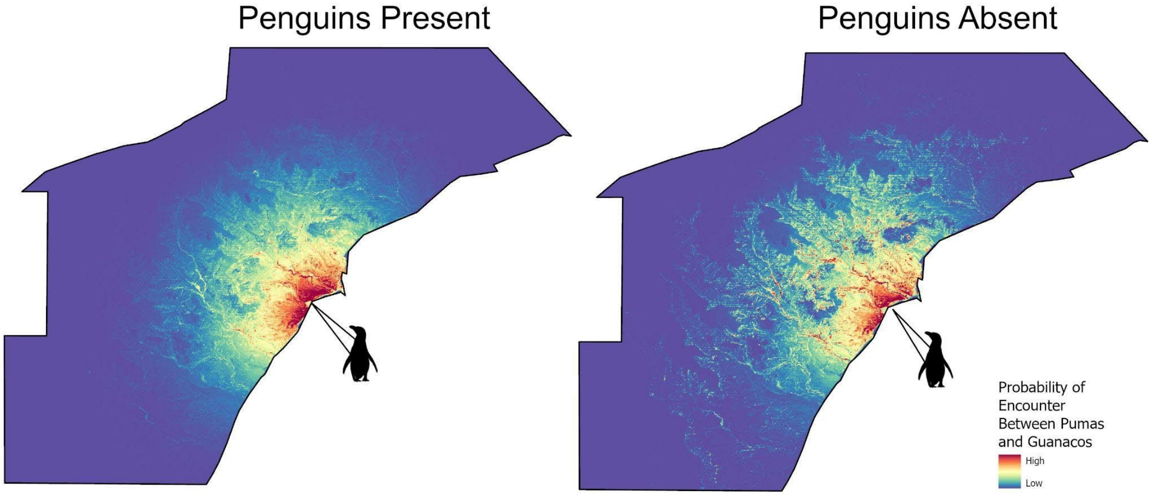


Fig 2. Boxplot of puma predation rates by diet type and season.

Encounter Probability

We identified 959 encounter events between collared pumas and collared guanacos. The spatial predictors for the probability of encounter were mostly consistent from season to season (Supplementary Data SD2; Supplementary Data SD3; Figure 3). For both seasons (penguin presence and absence), the top model indicated that encounter probability was higher closer to the penguin colony (penguins present: **β** = -2.07; 95% CI -2.22 - -1.92; penguins absent: **β** = -2.18; 95% CI -2.39 - -1.99), on steeper slopes (penguins present: **β** = 0.15; 95% CI 0.05 - 0.24; penguin absent: **β** = 0.34; 95% CI 0.23 - 0.46), and higher NDVI (penguins present: **β** = 0.33; 95% CI 0.24 - 0.44; penguins absent: **β** = 0.66; 95% CI 0.51 - 0.81). When penguins were absent, the top model also included a positive interaction between slope and NDVI (**β** = 0.15; 95% CI 0.04 - 0.28). Both models had relatively high continuous Boyce indices (penguins present = 0.94; penguins absent = 0.97).


Penguins Present

Penguins Absent

Fig 3. The predicted top model for the probability of encounter for pumas and guanacos across both seasons (penguins present and penguins absent) in MLNP. The top penguin presence model included distance to the penguin colony, slope, and NDVI. The top penguin absence model included distance to the penguin colony, slope, NDVI, and an interaction between slope and NDVI. The penguin silhouette indicates the location of the penguin colony.

Predation Risk

The spatial predictors of predation risk varied by season (Supplementary Data SD4; Supplementary Data SD5; Figure 4). When the penguins were present the top model indicated predation risk was higher at lower elevations (**β** = -0.40; 95% CI -0.58 - -0.22), greater NDVI (**β** = 1.24; 95% CI 1.06 - 1.43), and greater ruggedness (**β** = 0.27; 95% CI 0.09 - 0.44). However, when the penguins were absent the top model suggested higher predation risk closer to the penguin colony (**β** = -0.36; 95% CI -0.56 - -0.17) and at greater NDVI (**β** = 0.76; 95% CI 0.56 - 0.96). Both models had moderately high continuous Boyce indices (penguins present = 0.48; penguins absent = 0.58).

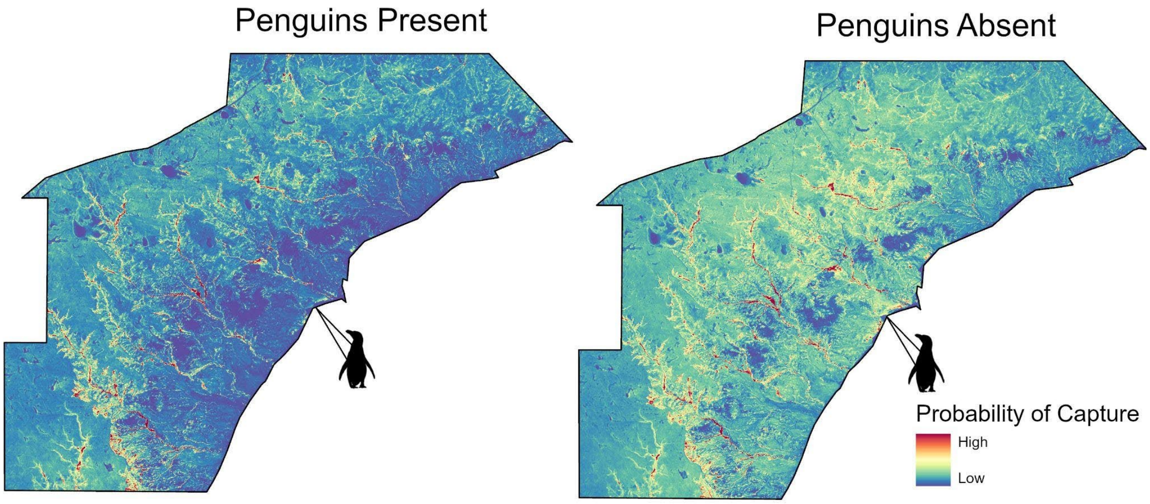


Fig 4. The predicted top model for puma capture probability of guanacos for both seasons (penguin presence and absence) across MLNP. The top penguin presence model included elevation, NDVI, and ruggedness. The top penguin absence model included distance to the penguin colony and NDVI. The penguin silhouette indicates the location of the penguin colony.

DISCUSSION

Wildlife recovery efforts around the world are working to restore predator populations and their ecological influence. However, human impacts can dramatically alter the landscape and resource dynamics resulting in changes to predator-prey interactions (Guiden et al., 2019). In this study, we find that human disruptions to animal communities have created the conditions for a novel predator-prey interaction between pumas and penguins, shifting predator-prey dynamics for the classic puma-guanaco system in coastal Patagonia. Our findings reveal that seasonal fluctuations in penguin presence alternately decrease and increase predation risk for the primary prey, guanacos. Additionally, consistent with the *Prey Catchability Hypothesis*, habitat features remain important drivers of predation risk across the landscape. These results highlight how novel environments can complicate the outcomes for restoring trophic interactions.

Our findings suggest that puma predation of guanacos is mediated seasonally by the presence and absence of penguins. This is evident by our improved ability to predict encounter and capture probability when accounting for the penguin colony. When penguins were available, predation risk for guanacos remained low near the colony despite a high likelihood of encounters. This suggests that pumas were either satiated or preferentially targeting the alternative prey. Conversely, predation risk for guanacos increased near the colony when penguins were absent. While individual pumas hunting penguins exhibited lower predation rates on guanacos compared to those specializing on guanacos, the increased aggregation of pumas near the colony appears to have elevated the overall predation risk for guanacos. Additionally, prey catchability remained a significant factor influencing predation risk across both seasons.

Denser vegetation offers concealment for pumas and areas with steeper slopes or rugged terrain facilitate ambush tactics. Previous studies of pumas and other ambush predators have also found capture probability to be the key driver influencing hunting behavior (Balme et al. 2007; Hopcraft et al. 2005; Smith et al. 2020). However, the observed increase in predation risk near the colony while penguins are absent highlights the limitations of solely considering the catchability of primary prey for explaining predation patterns.

The impacts of human influences along coastal Patagonia have given rise to a unique, multi-prey system, introducing complexities into our understanding of puma-guanaco interactions. Predators in multi-prey systems can adjust their habitat utilization or foraging tactics to exploit particular prey species, consequently influencing the predator-prey dynamics of other prey species within the ecosystem (Brunet et al., 2023; Higginson & Ruxton, 2015; Ross & Winterhalder, 2015). Despite the prevalence of multi-prey systems, most studies tend to oversimplify their scope to single predator-single prey systems (Montgomery et al. 2019). However, the presence of multiple prey species can significantly influence predation patterns across heterogeneous landscapes. The influence of alternative prey on predation risk may be particularly pronounced when accessing specific prey types presents strict spatial limitations.

For example, as cutthroat trout (*Oncorhynchus clarkii bouvieri*) declined in Yellowstone Lake, grizzly bears (*Ursus arctos*) reduced their visitation to trout streams and switched to predating neonate elk (*Cervus elaphus*) (Middleton et al., 2013; Teisberg et al., 2014). Similarly, the significant spatial adjustments required to exploit penguins likely contribute heavily to the observed shifts in predation risk at MLNP. Thus, for a comprehensive understanding of spatial predation patterns across heterogeneous landscapes, researchers must consider how the presence of multiple prey species influences predator behavior, distribution, and population dynamics.

Our study demonstrates the importance of deconstructing the predation sequence, revealing a seasonal decoupling between encounter probability and capture probability. While previous research documented reduced guanaco space use near the penguin colony, we observed high encounter rates near the colony irrespective of penguin presence. This elevated encounter rate likely stems from the increased puma aggregation and density facilitated by this marine subsidy (Chapter 3; Serota et al. 2023). However, a high encounter probability only translated to a high capture probability when the penguins were absent. The overlap between encounter probability and capture probability reflects a combined influence of the environment, predators, and prey. Thus, this mismatch gives us insight into the mechanism by which the penguin colony impacts the puma-guanaco interaction. When the penguins are available, puma encounters near the colony pose minimal risk to guanacos. During this time, pumas near the colony are likely satiated or not actively hunting due to preference for a more abundant and easily catchable resource.

Despite seasonal and spatial fluctuations in predation risk near the penguin colony, it remains unclear whether guanacos perceive or respond to these changes, and whether these changes overall impact the guanaco population. Given the high density of pumas, it is surprising that guanacos don’t completely avoid the area. However, there may be benefits that outweigh the risks for guanacos near the colony. These potential benefits may include access to nutrients transported by the penguin colony providing enhanced vegetation productivity or reduced competition with conspecifics (Acebes et al., 2013; Grant et al., 2022). Future research should further tease apart the spatial variation in guanaco perception of risk and its impacts on guanaco distribution and antipredator behavior (Gaynor et al. 2019). Additionally, while the spatial distribution of predation risk fluctuates seasonally, the overall predation risk at MLNP compared to other systems remains unclear. Many pumas within the park predate penguins, and their predation rate of guanacos was nearly two times lower compared to pumas that don’t predate penguins. Despite an abundant puma population, it’s uncertain if the higher number of pumas compensates for the lower individual predation rate on guanacos. Comparisons of guanaco mortality rates and population trajectories across Patagonia will lead to a better understanding of how penguins mediate the puma-guanaco interaction.

Our findings illuminate the growing challenge of understanding predator-prey interactions within increasingly modified ecosystems. Restoring the ecological influence of predators through their trophic interactions is often the central aim of predator conservation, but in a highly modified landscape like MLNP with novel prey species like penguins, the ecological outcome of predator restoration can be hard to predict (Ladouceur et al., 2022; Perino et al., 2019). This study demonstrates how a novel prey species disrupts the trophic interaction between an apex predator and its primary prey, and how the broader ecological consequences of such a novel interaction remain unanswered. Future research should investigate whether this dynamic influences the landscape of fear for guanacos, triggers an ecological release and increased herbivory away from the colony, or results in apparent competition between guanaco and penguin populations. By disentangling these predator-prey dynamics, we can further our understanding of how anthropogenic influences reshape their environments and how novel environments can shape the outcomes of predator conservation and restoration efforts.

SUPPLEMENTARY DATA

Supplementary Data SD1: Predation rates for each individual puma.

ID	Diet	Days Monitored	Predation Events	Weekly Predation Rate (Penguins Present)	Weekly Predation Rate (Penguins Absent)
MLP1	No Penguin	161	18	0.754902	0.830508
MLP10	No Penguin	74	5	0.472973	na
MLP11	No Penguin	574	59	0.720588	0.717949
MLP12	No Penguin	453	59	0.869697	1.02439
MLP13	Penguin	421	21	0.234899	0.626016
MLP14	Penguin	422	21	0.140468	0.739837
MLP15	No Penguin	103	14	1.037037	0.921053
MLP2	Penguin	127	8	0.424242	0.459016
MLP3	Penguin	676	45	0.4375	0.518519
MLP4	Penguin	576	25	0.275758	0.284553
MLP5	No Penguin	488	33	0.474576	0.470149
MLP7	Penguin	360	19	0.295359	0.170732

MLP8	Penguin	548	22	0.12426	0.533333
MLP9	Penguin	579	23	0.21021	0.199187

Supplementary Data SD2: AICc, LL, K, Covariates for puma-guanaco encounter model while the penguins were present

Model	Covariates	K	AICc	ΔAICc	Log Likelihood
14	Penguin Colony + NDVI + Slope	4	2723.7	0	-1357.88
22	Penguin Colony + NDVI + TRI	4	2723.8	0.1	-1357.88
86	Penguin Colony + NDVI + TRI + NDVI:TRI	5	2724.3	0.6	-1357.18
46	Penguin Colony + NDVI + Slope + NDVI:Slope	5	2724.5	0.8	-1357.27
6	Penguin Colony + NDVI	3	2731.8	8.1	-1362.94
10	Penguin Colony + Slope	3	2773.2	49.5	-1383.62
18	Penguin Colony + TRI	3	2773.3	49.6	-1383.69
2	Penguin Colony	2	2775.7	52.0	-1385.89
15	Elevation + NDVI + Slope	4	3255.3	531.6	-1623.66
23	Elevation + NDVI + TRI	4	3255.5	531.8	-1623.77

47	Elevation + NDVI + Slope + NDVI:Slope	5	3256.9	533.2	-1623.49
87	Elevation + NDVI + TRI + NDVI:TRI	5	3257.0	533.3	-1623.5
11	Elevation + Slope	3	3286.7	563.0	-1640.38
19	Elevation + TRI	3	3287.2	563.5	-1640.62
7	Elevation + NDVI	3	3294.7	571.0	-1644.38
3	Elevation	2	3316.6	592.9	-1656.31
45	NDVI + Slope + NDVI:Slope	4	3830.6	1106.9	-1911.33
85	NDVI + TRI + NDVI:TRI	4	3832.1	1108.4	-1912.09
13	NDVI + Slope	3	3837.9	1114.2	-1915.98
21	NDVI + TRI	3	3840.4	1116.6	-1917.2
9	Slope	2	3843.8	1120.1	-1919.91
17	TRI	2	3846.3	1122.6	-1921.17
5	NDVI	2	3869.6	1145.9	-1932.82

Supplementary Data SD3: AICc, LL, K, Covariates for puma-guanaco encounter model for when the penguins were absent.

Model	Covariates	K	AICc	ΔAICc	Log Likelihood
46	Penguin Colony + NDVI + Slope + NDVI:Slope	5	1571.5	0	-780.7
86	Penguin Colony + NDVI + TRI + NDVI:TRI	5	1573.7	2.2	-781.8

14	Penguin Colony + NDVI + Slope	4	1577.1	5.5	-784.5
22	Penguin Colony + NDVI + TRI	4	1578.5	6.9	-785.2
6	Penguin Colony + NDVI	3	1608.1	36.5	-801.0
10	Penguin Colony + Slope	3	1689.1	117.5	-841.5
18	Penguin Colony + TRI	3	1690.9	119.4	-842.4
2	Penguin Colony	2	1710.1	138.5	-853.0
47	Elevation + NDVI + Slope + NDVI:Slope	5	2088.0	516.4	-1039.0
87	Elevation + NDVI + TRI + NDVI:TRI	5	2090.8	519.2	-1040.4
15	Elevation + NDVI + Slope	4	2098.3	526.7	-1045.1
23	Elevation + NDVI + TRI	4	2100.9	529.3	-1046.4
11	Elevation + Slope	3	2165.7	594.1	-1079.8
19	Elevation + TRI	3	2168.7	597.1	-1081.3
7	Elevation + NDVI	3	2182.7	611.2	-1088.3
3	Elevation	2	2231.7	660.1	-1113.8
45	NDVI + Slope + NDVI:Slope	4	2443.3	871.7	-1217.6
85	NDVI + TRI + NDVI:TRI	4	2446.6	875.0	-1219.3
13	NDVI + Slope	3	2459.7	888.1	-1226.8
9	Slope	2	2460.9	889.3	-1228.4
21	NDVI + TRI	3	2463.3	891.7	-1228.6

17	TRI	2	2464.7	893.1	-1230.3
5	NDVI	2	2550.5	978.9	-1273.2

Supplementary Data SD4: AICc, LL, K, Covariates for capture probability model for when the penguins were present

Model	Covariates	K	AICc	ΔAICc	Log Likelihood
23	Elevation + NDVI + TRI	4	991.2	0.0	-491.6
15	Elevation + NDVI + Slope	4	991.5	0.3	-491.8
47	Elevation + NDVI + Slope + NDVI:Slope	5	991.6	0.4	-490.8
87	Elevation + NDVI + TRI + NDVI:TRI	5	992.0	0.8	-491.0
46	Penguin Colony + NDVI + Slope + NDVI:Slope	5	997.9	6.7	-493.9
22	Penguin Colony + NDVI + TRI	4	998.0	6.8	-495.0
14	Penguin Colony + NDVI + Slope	4	998.2	7.0	-495.1
7	Elevation + NDVI	3	998.2	7.0	-496.1
86	Penguin Colony + NDVI + TRI + NDVI:TRI	5	998.5	7.3	-494.2
6	Penguin Colony + NDVI	3	1001.9	10.7	-498.0
45	NDVI + Slope + NDVI:Slope	4	1009.1	17.8	-500.5
21	NDVI + TRI	3	1009.2	18.0	-501.6
13	NDVI + Slope	3	1009.4	18.2	-501.7

85	NDVI + TRI + NDVI:TRI	4	1009.7	18.5	-500.8
5	NDVI	2	1014.7	23.4	-505.3
3	Elevation	2	1207.0	215.8	-601.5
9	Slope	2	1207.1	215.9	-601.6
17	TRI	2	1207.2	216.0	-601.6
2	Penguin Colony	2	1207.8	216.5	-601.9
11	Elevation + Slope	3	1208.3	217.0	-601.1
19	Elevation + TRI	3	1208.3	217.1	-601.2
10	Penguin Colony + Slope	3	1209.1	217.9	-601.6
18	Penguin Colony + TRI	3	1209.2	218.0	-601.6

Supplementary Data SD5: AICc, LL, K, Covariates for capture probability model for when the penguins were absent

Model	Covariates	K	AICc	ΔAICc	Log Likelihood
6	Penguin Colony + NDVI	3	1012.3	0.0	-503.1
22	Penguin Colony + NDVI + TRI	4	1014.1	1.8	-503.0
14	Penguin Colony + NDVI + Slope	4	1014.1	1.9	-503.1
7	Elevation + NDVI	3	1015.4	3.2	-504.7
46	Penguin Colony + NDVI + Slope + NDVI:Slope	5	1015.9	3.6	-502.9
86	Penguin Colony + NDVI + TRI +	5	1016.0	3.7	-503.0

	NDVI:TRI				
23	Elevation + NDVI + TRI	4	1016.1	3.8	-504.0
15	Elevation + NDVI + Slope	4	1016.1	3.9	-504.1
47	Elevation + NDVI + Slope + NDVI:Slope	5	1017.8	5.5	-503.9
87	Elevation + NDVI + TRI + NDVI:TRI	5	1017.8	5.6	-503.9
5	NDVI	2	1026.7	14.4	-511.3
21	NDVI + TRI	3	1027.7	15.5	-510.9
13	NDVI + Slope	3	1027.8	15.5	-510.9
45	NDVI + Slope + NDVI:Slope	4	1029.5	17.3	-510.7
85	NDVI + TRI + NDVI:TRI	4	1029.6	17.4	-510.8
2	Penguin Colony	2	1071.8	59.6	-533.9
18	Penguin Colony + TRI	3	1073.7	61.4	-533.8
10	Penguin Colony + Slope	3	1073.7	61.5	-533.8
3	Elevation	2	1074.4	62.1	-535.2
11	Elevation + Slope	3	1076.4	64.1	-535.2
19	Elevation + TRI	3	1076.4	64.1	-535.2
9	Slope	2	1077.8	65.6	-536.9
17	TRI	2	1077.8	65.6	-536.9

Chapter 6. Concluding Remarks

As biodiversity continues to decline around the world, the need to find solutions that promote the successful restoration of wildlife has become increasingly clear. However, the success and ecological outcomes of wildlife restoration efforts have varied widely. The work presented in this dissertation highlights that 1) the success of wildlife restoration hinges on community buy-in, stakeholder involvement, and the incorporation of human dimensions, and 2) novel environments can lead to novel species interactions which can drastically impact the ecological outcomes of restoration efforts.

A major question for wildlife recovery in novel ecosystems is whether ecosystems can return to their original state (Hobbs et al., 2024; Stier et al., 2016). Human activity and influences can impact species compositions, interactions, and ecological processes that tip ecosystems into alternative states (Beisner et al., 2003). Novel ecosystems like MLNP represent an alternative state, where the structure, function, and species composition differ from those of its "historical" state. However, does the restoration of wildlife reverse the effects of their absence and return ecosystems to its state prior to the extirpation of that target species? Perhaps for novel ecosystems, we may be more likely to see hysteresis, whereby ecosystems fail to return to their original state (Stier et al., 2016). Since MLNP was established, the penguin colony has only increased in abundance, suggesting a sustainability to puma predation on penguins (Millones et al., 2022). Questions remain about the long-term viability of this interaction, including the effects of penguin metapopulation dynamics, the number of pumas the colony can sustain, predation on different penguin age classes, and the total number of penguins predated each year. Still, given the penguin population trajectory thus far, it's possible that MLNP will remain in an alternative state with pumas, penguins, and guanacos. In this alternative state, puma behavior and density is heavily dependent on the penguin colony, and puma predation of guanacos is seasonally mediated by penguins. Restoration efforts at MLNP are in their early stages and ongoing, so we still need more time to understand how this ecosystem responds.

Restoring wildlife to novel ecosystems presents unique challenges for conservation and management: what are the ultimate objectives, and what philosophy should guide these efforts? This dissertation reveals that novel ecosystems can: 1) alter herbivore foraging patterns, shifting their distribution across the landscape; 2) create resource pulses that shape predator behavior and population dynamics; and 3) fundamentally reshape the spatial patterns of predator-prey interactions. Altered herbivory and predator-prey dynamics are known to trigger cascading ecological effects (Estes et al., 2011). Given this understanding, it's likely that changes observed in consumer interactions at MLNP are impacting the ecosystem's structure and function. Many of the major wildlife restoration paradigms and frameworks stress the restoration of trophic interactions to improve ecosystem structure and function (Loch et al., 2020; Perino et al., 2019). In fact, the restoration of predators around the world are often sold and predicated on their ability to restore ecosystems. However, novel ecosystems have been shown to weaken the ecosystem effects of other wildlife restoration efforts, including the well-documented wolf restoration observed in North America and Europe (Hobbs et al., 2024; Kuijper et al., 2024). While there are many valid reasons to restore predators, we should not automatically assume that restoring ecosystems is one of them. Taken together, these results highlight the unpredictability of wildlife restoration outcomes in novel ecosystems, prompting important questions about target-setting within the conservation community. Ultimately, for future wildlife restoration efforts, how can we develop forward-looking objectives and targets that account for the potential emergence, ongoing presence, and stability of novel interactions and their ecological consequences?

Most, if not all, ecosystems have some degree of novelty. It is undoubtedly important to both think critically about and invest in understanding how recovering species are adapting to their novel environments. Still, we must collectively recognize that novel ecosystems are here to stay. Given the amount of human influence on our planet, it is unlikely that we will ever return most ecosystems to their original state. Acceptance of this fact may allow us to better design conservation measures and continue to reverse the decline of biodiversity worldwide.

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