UC Berkeley
UC Berkeley Electronic Theses and Dissertations

Title

From home ranges to range-level connectivity: conservation and behavioral insights from GPS telemetry data

Permalink

https://escholarship.org/uc/item/9zd7b925

Author

Karandikar, Harshad Hemant

Publication Date

2023

Peer reviewed|Thesis/dissertation

From home ranges to range-level connectivity:
conservation and behavioral insights from GPS telemetry data

by

Harshad Hemant Karandikar

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Arthur D. Middleton, Chair
Professor Claire Kremen
Professor Justin Brashares
Professor Eileen Lacey

Summer 2023

From home ranges to range-level connectivity:
conservation and behavioral insights from GPS telemetry data

Copyright 2023

By

Harshad Hemant Karandikar

Abstract

From home ranges to range-level connectivity:
conservation and behavioral insights from GPS telemetry data

by

Harshad Hemant Karandikar

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Arthur D. Middleton, Chair

Understanding how animals use space and access key resources can offer critical insights that can inform management and conservation actions. This dissertation explores space use and movement behavior for three large mammalian species in South America at different scales and with different emphases. In Chapter 1, I study vicuña space use in the southern end of the species' range and compare this with results from other parts of the vicuña range. My study offers the first estimates of vicuña home range sizes using telemetry data and compares these with results from previous studies. Additionally, I assess how vicuñas at my study site share space with conspecifics from other families, and if vicuñas display the strong territorial behavior displayed by the species in other parts of their range. Finally, I investigate how environmental factors may affect vicuña space use, including home range sizes, space-sharing and diel migration patterns. In Chapter 2, I study puma space use in three protected areas in the high Andean and Patagonian steppes and answer questions about the linkages between heterogeneity in the landscape and how pumas use space and move around in their home ranges. As a carnivore species known for its flexibility in adapting to very different habitat conditions, do pumas respond to differences in habitats and terrain factors with changes in behavior? What are the specific ways in which varying landscape variables affect this space use? Do different landscape factors affect behavior across study sites? Does changing landscape heterogeneity affect other factors such as distances moved by pumas? Chapter 3 comprises an assessment of connectivity between key jaguar habitats. First, I use a large, publicly available jaguar GPS telemetry dataset to develop a movement resistance layer, incorporating key environmental and anthropogenic variables known to facilitate or impede jaguar movement across the species' range in the Americas. Next, I identify corridor areas connecting key jaguar habitats and other protected areas that are likely to be important from a jaguar conservation perspective across the jaguar range. These identified corridors may offer important strategic inputs towards range-level jaguar conservation strategies to ensure connectivity and dispersal between jaguar populations. Together, these analyses offer behavioral and ecological insights that can inform conservation and management actions for continued persistence of these species and their movement across landscapes.

Dedicated to

Aai and *Baba*

and to

Branca: May your spirit rule over the majestic steppe for eternity

Table of Contents

Acknowledgements

company and fun times, and to Sasha Nikolaeva for the innumerable runs around Berkeley and the venting sessions when things seemed to be going off the rails. Thank you to Christine Wilkinson for being an amazing friend and travel buddy. Thank you to the GSAOs who have patiently supported me during my time in the department; in particular, Bianca Victorica and Ryann Madden.

A big thank you to Emiliano Donadio of Rewilding Argentina for the immense support and encouragement, and amazing research advice, at a time when I was well and truly lost, in addition to always doing everything he could to make field work in the Patagonian steppe possible, to Andres Navaro for his incredible dedication and passion for doing phenomenal work on human-wildlife coexistence in the Patagonian steppe and for letting me be a part of that till Covid unraveled all of my grand plans, and to Robin Naidoo from WWF-US for his mentorship and encouragement for the third chapter of this dissertation. Special thanks to Pablo Alarcon for all the memories of that insane field season in Laguna Blanca and getting the field truck unstuck the half a dozen times that it seemed to happen every single day; a task that I was hopelessly useless at, and also for driving fast enough for us to get away during that midnight car chase.

Thank you to Sejal Worah, Dipankar Ghose, and Vishaish Uppal for taking a chance on me at WWF-India, and later, Yash Shethia for being an amazing boss and colleague. Thank you to all of my other incredible colleagues at WWF-India who made my journey there memorable.

I am grateful to the incredible written works of Gerald Durrell, and to my school library for including them in the school collection. This was the kindling to the spark that Aai generated in me by dragging me to all those birdwatching expeditions at ungodly hours on foggy winter mornings in my hometown.

Lastly, I want to acknowledge the importance of a quote that has continued to inspire me for over a decade, especially when I had to take the leap of faith that actually got me into working in wildlife conservation:

"They deem me mad because I will not sell my days for gold; and I deem them mad because they think my days have a price."

- *Kahlil Gibran*

Introduction

Advances in GPS and battery technology have led to an explosion in availability of wildlife telemetry data (Nathan et al. 2022) that has the potential to transform the field of wildlife ecology (Kays et al. 2015; Wilmers et al. 2015). At the same time, significant strides have been made in reducing barriers to accessing planet-scale satellite datasets for environmental, anthropogenic, and climatological variables that likely drive animal movement and behavior, especially through the advent of platforms like Google Earth Engine (Gorelick et al. 2017; Kumar and Mutanga 2018). The relative ease with which large terrestrial mammalian species can be collared offers us an unprecedented opportunity to understand the behavior and ecology of these species, many of which face a myriad variety of threats, including, amongst other things, habitat loss, pressures from the wildlife trade and retaliation due to conflict with humans (Cardillo et al. 2005; Ripple et al. 2017). Developing a baseline understanding of how animals use space, including for specific activities such as foraging, predation, and long-range dispersal, may offer critical insights for developing conservation and management strategies that address these threats and work towards landscapes where people and wildlife can co-exist in a sustainable way.

In this dissertation, I assess animal space use and behavior at different scales, starting at the home range level and building up to a species' range level analysis. In a sense, this 'scaling up' mirrors my journey as a movement ecologist who uses GPS telemetry data to understand animal behavior and ecology with an objective of informing conservation strategies and actions. I start with an analysis of the spatial ecology of the vicuña (*Vicugna vicugna*) in Chapter 1, a diminutive camelid found in the high Andes, in San Guillermo National Park, a remote protected area in the southern end of the species' range. Although the subject of some of the foundational studies of territoriality and space-sharing in ungulates (Koford 1957; Franklin 1974), vicuña space use and behavior has not been systematically assessed with modern telemetry techniques. In this chapter, I offer the first assessment of vicuña spatial ecology and space-sharing using data obtained from GPS collars, with an objective of evaluating previous assertions made about territoriality for the species. We found evidence of considerable space-sharing of foraging areas between collared vicuñas that belonged to distinct, separate family groups. In several instances, multiple collared vicuñas from separate family groups were observed foraging in close proximity to one another, suggesting an absence of the strict territorial behavior previously ascribed to the species at least during some spatial and temporal windows. Given the strong differences in environmental conditions, especially precipitation, in our study site compared to the rest of the vicuña range, we conclude that in line with observations made for other ungulate species, vicuñas display plasticity in social behavior, including tolerance of conspecifics, with changing environmental conditions and resource availability.

In Chapter 2, I analyze the role of landscape heterogeneity in influencing space use, including all-use locations, predation sites and daily movements of an apex predator, the puma (*Puma concolor*), across three sites in the high Andean and Patagonian steppes. Pumas are generally considered to be ambush or sit-and-pursue predators that avoid chasing prey over long distances Murphy et al. 1998; Ruth and Murphy 2009), as opposed to coursing predators that may use significantly larger areas within the landscape to hunt. Pumas are also known for their remarkable flexibility, reflected through their ability to inhabit extremely different environments

and habitats and survive on a wide variety of prey species across taxonomic groups (Karandikar et al. 2022). I assessed how this flexibility might impact space use patterns with changing landscape conditions and found that increasing landscape heterogeneity was associated with lower levels of clustering of locations used by pumas, including predation sites and other locations. Pumas in highly homogeneous landscapes thus are likely to limit their activity to small areas within their home range that likely support their ambush hunting strategy, as opposed to more heterogeneous landscapes that likely offer a considerably larger and well-distributed number of such suitable sites. A similar trend was observed in the daily movement rates: pumas in the low heterogeneity high Andean site moved significantly shorter distances than pumas in the sites in the Patagonian steppe. These differences in behavior can have dramatic effects on landscapes (Monk and Schmitz 2022) and may be an important factor in managing the species, especially in working landscapes.

Chapter 3 comprises an assessment of connectivity between important areas that support viable jaguar populations across the range of the species, from northern Mexico to north-central Argentina. This analysis builds upon previous work (Rabinowitz and Zeller 2010; Zeller et al. 2013) by incorporating a publicly available dataset of over a hundred individual jaguars across the species' range (Morato et al. 2018), with an objective of identifying specific corridors that need to be safeguarded to allow dispersing jaguars to move between these areas. These identified corridors can help inform on-the-ground actions and strategies for jaguar conservation across the Americas.

References

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R., Sechrest, W., Orme C. D. L & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, *309*(5738), 1239-1241.

Franklin, W. L. (1974). The social behaviour of the vicuña. *The behaviour of ungulates and its relation to management*, *1*, 477-487.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote sensing of Environment*, 202, 18-27.

Karandikar, H., Serota, M. W., Sherman, W. C., Green, J. R., Verta, G., Kremen, C., & Middleton, A. D. (2022). Dietary patterns of a versatile large carnivore, the puma (Puma concolor). *Ecology and Evolution*, *12*(6), e9002.

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478.

Koford, C. B. (1957). The vicuña and the puna. *Ecological monographs*, *27*(2), 153-219.

Kumar, L., & Mutanga, O. (2018). Google Earth Engine applications since inception: Usage, trends, and potential. *Remote Sensing*, *10*(10), 1509.

Monk, J. D., & Schmitz, O. J. (2022). Landscapes shaped from the top down: predicting cascading predator effects on spatial biogeochemistry. *Oikos*, 2022(5), e08554.

Morato, R. G., Thompson, J. J., Paviolo, A., de La Torre, J. A., Lima, F., McBride Jr, R. T., ... & Ribeiro, M. C. (2018). Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics.

Murphy, K. M. (1998). *The ecology of the cougar (Puma concolor) in the northern Yellowstone ecosystem: interactions with prey, bears, and humans*. University of Idaho.

Nathan, R., Monk, C. T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C. E., Bertram, M. G., Bijleveld, A. I., Brodin, T., Brooks, J. L., Campos-Candela, A., Cooke, S. J., Gjelland, K. Ø., Gupte, P. R., Harel, R., Hellström, G., Jeltsch, F., … Jarić, I. (2022). Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*, *375*(6582), eabg1780.

Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. *Biological conservation*, *143*(4), 939-945.

Ripple, W. J., Wolf, C., Newsome, T. M., Hoffmann, M., Wirsing, A. J., & McCauley, D. J. (2017). Extinction risk is most acute for the world's largest and smallest vertebrates. *Proceedings of the National Academy of Sciences*, *114*(40), 10678-10683.

Ruth, T. K., & Murphy, K. (2009). Cougar-prey relationships. *Cougar: Ecology and Conservation. The Univ. of Chicago Press, Chicago*, 138-155.

Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, *96*(7), 1741-1753.

Zeller, K. A., Rabinowitz, A., Salom-Perez, R., & Quigley, H. (2013). The jaguar corridor initiative: a range-wide conservation strategy. *Molecular population genetics, evolutionary biology and biological conservation of neotropical carnivores. Nova Science Publishers, New York*, 629-658.

Chapter 1: Spatial ecology of the vicuña (*Lama vicugna*) in a high Andean protected area

This chapter has been previously published in the Journal of Mammalogy.

Abstract

The study of animal space use is fundamental to effective conservation and management of wildlife populations and habitats in a rapidly changing world, yet many species remain poorly described. Such is the case for the spatial ecology of the Vicuña–a medium-sized wild camelid that plays a critical role, both as a consumer and as prey, in the high Andean food web. We studied patterns of space use of 24 adult female vicuñas from April 2014 to February 2017 at the southern edge of its range. Vicuñas showed strong fidelity to their home range locations across the study period and shared large portions of their home ranges with vicuñas from other family groups. Vicuña home ranges in our study were considerably larger than previous estimates across the range of the species. Variation in environmental and terrain factors and the associated risk of predation affected vicuña diel migration distance but not home range size or overlap. Our study offers new ecological insights into vicuña space use that can inform conservation and management efforts of vicuñas and other social ungulates.

Introduction

Conserving ungulates and their ecological roles requires comprehensive understanding of their behavior, natural history, and space use–however, many species have not been adequately described to facilitate targeted conservation approaches. Within ungulates, considerable diversity exists in space use, including nomadic behavior without site fidelity, home ranges without territoriality, lekking, year-round territoriality, and seasonal territoriality (Lott 1991)–driven by factors including behavioral and genetic plasticity and a multitude of environmental and ecological variables affecting space use (Maher and Lott 2000). Such variation in space use and social structure signifies the wide range of habitat requirements across species. Understanding animal space use, especially the common yet complex phenomena of home ranging behavior and territoriality (Owen-Smith 1977), is fundamental to effective conservation and management of wildlife populations and habitats in a rapidly changing world.

The Vicuña (*Lama vicugna*) is a medium-sized wild camelid endemic to the high Andes of South America (Koford 1957; Franklin 1974) that plays a critical role in the high Andean food web and is an important food item for carnivores (Donadio et al. 2010; Donadio and Buskirk 2016) and scavengers (Perrig et al. 2017). The Vicuña is the most abundant large herbivore in the region and has important effects on the plant community (Donadio and Buskirk 2016). Indiscriminate hunting in the 19th and 20th centuries led to a precipitous decline in vicuña populations across their range, before the species received legal protection under the Convention for the Conservation and Management of the Vicuña in 1979 and recovered in many areas during the late 20th century (McNeill et al. 2009). While the northern subspecies of the Vicuña, *L. v.*

4

mensalis, is no longer in danger of extinction, the southern subspecies, *L. v. vicugna*, is still threatened (Bonacic and Gimpel 2003; Acebes et al. 2018). Many wild vicuña populations continue to be highly managed or are otherwise impacted by human use of the landscape (McLaren et al. 2018). In some areas, vicuñas are periodically captured and sheared for their highly valued fiber, which can alter social behavior (Bonacic and Galaz 2001; but see Arzamendia et al. 2018) and increase stress levels (Bonacic and Macdonald 2003). Attempts have even been made to hybridize vicuñas and alpacas (*L. pacos*) to improve fiber quality and production (Lichtenstein 2009). More recently, outbreaks of mange, a highly contagious disease caused by mites (*Sarcoptes scabiei*), have heavily impacted some populations (Monk et al. 2022).

Previous studies on vicuña space use and social behavior, based on visual observation of known individuals, have suggested that family group territories are exclusive and well-defended, with high site fidelity (Koford 1957; Franklin 1974; Bosch and Svendsen 1987; Arzamendia et al. 2018). Other studies, however, contend that vicuña families tend to tolerate some territory overlap (Vilá 1994) and that territoriality is not universal in the species (Vilá and Roig 1992; Cassini et al. 2009). Vicuñas are usually sedentary (i.e., do not undertake seasonal migrations) and tend to only use small portions of available suitable habitat (Cassini et al. 2009). Increased mobility in some vicuña populations has been ascribed to human disturbance (Vilá 2000). About 60% of vicuñas live in Permanent Territorial Family groups (Franklin 1974, 1976) that generally comprise one male, three to four females, and one to two offspring (Cassini 2009). Vicuña families have also been reported to maintain distinct feeding (day) and sleeping (night) territories (Franklin 1974), although other studies suggest that this behavior may not be universal (Koford 1957; Menard 1982). While data obtained through visual observations offer critical information about behavior that is impossible to determine using remotely sensed locational information (e.g., definitive evidence about territory defense and thus territoriality), advances in biologging technologies now allow for more fine-scale, continuous, and comprehensive analysis of animal space use (Kays et al. 2015; Wilmers et al. 2015) compared to the limited number of observations possible through visual methods.

We aim to investigate space use in a population of wild, unmanaged vicuñas using the first available GPS location data set for the species and compare this with the current understanding of vicuña spatial ecology. The main objectives of this work are to: (1) offer the first estimates of vicuña home range sizes using GPS locations and understand the relationship between forage availability, family group size, and home range size; and (2) assess the impact of environmental factors on home range size, overlap, and diel migrations. Environmental conditions, including resource availability and distribution, may affect ungulate space use and space sharing. The habitat productivity hypothesis, for example, suggests that ungulate home ranges tend to be smaller in areas with higher productivity (Harestad and Bunnel 1979; Seigle-Ferrand et al. 2021), whereas the resource dispersion hypothesis supports home range sharing when forage availability is limited and highly clumped (Johnson et al. 2002). Environmental conditions may also impact daily movements, with diel migrations previously reported in the system (Smith et al. 2019a). Vicuñas in our study system used two distinct, mutually exclusive areas, offering a unique opportunity to contrast behavioral and space use differences associated with varying environmental conditions within the same broader landscape. At the study system level, environmental conditions differ considerably from other areas in the vicuña range, offering an

opportunity to understand vicuña space use and examine the differences in space use and behavior in differing environments.

First, we estimate vicuña home range sizes and test the relationships between range size and environmental factors and family size. We then investigate differences in range sizes across seasons (growing and nongrowing) and sites. We hypothesize that differences in vegetation and terrain–including forage availability and distribution, elevation, and slope–lead to differences in space use. We predict that vicuña home ranges will be smaller in the site with higher forage availability and during the growing period. Next, we investigate space sharing between vicuñas. We hypothesize that environmental conditions affect space sharing and predict that: (a) vicuña ranges will generally overlap due to the limited availability and clumped distribution of forage; and (b) range overlap will decrease in the growing period due to increased forage availability. Finally, we investigate vicuña diel migrations between day and night ranges. We hypothesize that vicuñas adjust their daily movements in response to environmental conditions. We predict that: (a) vicuñas in the site with less heterogeneity will move longer daily distances; and (b) vicuñas will move longer daily distances in the nongrowing periods due to reduced availability of forage.

Materials & Methods

Study area and species: The study was conducted in San Guillermo National Park, San Juan Province, Argentina, between April 2014 and February 2017. The park is at the southern edge of the vicuña range and is located in a remote part of the central Andes mountains (29°14′S, 69°21′W), with limited access to visitors and consequently very low levels of human disturbance (Donadio and Buskirk 2006). The park is in a semiarid region at an altitude of 2,000–5,600 m, with rainfall largely limited to a period from January to March, leading to a narrow growing season in mid and late summer (Salvioli 2007; Donadio et al. 2012). Three main habitat types characterize the park: medium-altitude plains, steep canyons, and meadows. The plains and canyons comprise a total of 96% of the park area, whereas the meadows that exist in patches in the plains or near drainage features comprise of 4% of the area (Donadio and Buskirk 2016). Meadows contain fertile soils and high moisture levels with species such as *Juncus* spp., *Carex* spp., *Scirpus* spp., and *Festuca* spp.–whereas the other areas are dominated by perennial *Jarava* spp. and *Stipa* spp. grasses (Donadio and Buskirk 2016). Population densities in the park at the time of our study were estimated at 9.5–12.7 vicuñas/km^2 (Donadio et al. 2012). guanacos (*L. guanicoe*) are considerably less abundant in the landscape, occurring at densities of 1 guanaco/km^2 (Puig and Videla 2007).

We deployed GPS collars (GPS 6000SD, Lotek) on 24 adult female vicuñas under permit #DCM 455 and subsequent renewals issued by the Administración de Parques Nacionales, Argentina. Prior to collaring, vicuñas were observed to identify animals from distinct family groups. Vicuña family groups were observed to be very cohesive and moved together when approached for darting. Vicuñas were darted from a truck or by approaching them slowly on foot, from distances ranging between 15–42 m. Carfentanil (0.03–0.06 mg/ kg) with Naltrexone (100 mg Naltrexone/1 mg Carfentanil) and Thiafentanil oxalate (0.06–0.1 mg/kg) antagonized with Naltrexone (10 mg Naltrexone/1 mg Thiafentanil) were used. Established mammal handling guidelines (Sikes and gannon 2011) were followed during animal capture and handling. The 24 vicuñas consisted of 13 and 11 females collared, respectively, in two sites within the park: (1)

Llano de los Leones in the north; and (2) San Guillermo Canyon in the center of the park. Llano de los Leones comprises a large meadow with high forage availability within a large open plain with low productivity, with an elevation range of 3,360–4,031 m and low average slope angle. The San Guillermo Canyon, with an elevation range of 3,312–3,925 m, had higher forage availability but with a more heterogeneous distribution. San Guillermo Canyon also had higher heterogeneity in elevation and slope (Smith et al. 2019b). We conducted our analyses with a total of 95,872 location points from 24 individual vicuñas using a 3-hour fix rate. Not all animals were monitored for the duration of the study period–the start and end dates of location data available for each vicuña are listed in Supplementary Data SD1.

Vicuña group composition, size, and site fidelity: Group composition and size were documented during and after collaring of vicuñas. Although previous studies on the species indicate strong territorial behavior, we first conducted a site fidelity analysis for each vicuña to establish a quantitative basis for home range studies, using Mean Squared Distance and Linearity Index as metrics (Munger 1984). Site fidelity analysis compares differences between actual movements and multiple random walks (Spencer et al. 1990). We used the *reproducible home ranges* (rhr) package (Signer and Balkenhol 2015) in R for this initial analysis. We used the range shift test in the *marcher* package (Gurarie and Cheraghi 2017) to check for migratory behavior and range shifts. In cases where the range shift test could not offer conclusive evidence for the absence of a range shift, we calculated the migration distance and range shift index metrics (Gurarie et al. 2017) using the *marcher* package (Gurarie and Cheraghi 2017).

Home range estimation: Vicuña home ranges were calculated separately across the study period, for different seasons and periods of the day (explained below). The adaptive local convex hull (a-LoCoH) method was primarily used for determining vicuña home ranges. The LoCoH method was favored over other home range estimators to calculate home range size because it more tightly outlines the areas utilized by the focal animal (Getz and Wilmers 2004), important from the perspective of understanding home range overlap. Of the three LoCoH approaches, we used the a-LoCoH method, as it is considered superior to the r and k methods (Getz et al. 2007). Optimal kernel parameter (*a*) values were determined for each vicuña by calculating home range areas for multiple values of *a* and selecting the value where the home range size–number of recorded locations curve tends to asymptote (Ryan et al. 2006; Fletcher and Fortin 2018). We used the heuristic value for *a* for some individuals where the optimal value could not be determined through the plots (Getz et al. 2007). In addition, we also calculated core ranges using 50% minimum convex polygon (MCP) and autocorrelated kernel density estimation (AKDE; Fleming et al. 2015) to enable better comparison with earlier studies on vicuñas.

Overall and seasonal ranges: Vicuña home ranges were estimated in four ways: (1) 50% day ranges for the study period (henceforth referred to as overall core ranges), using day locations for the entire duration of the study; (2) 95% day ranges for each season (referred to as seasonal home ranges); (3) 50% day ranges for each season (referred to as seasonal core ranges); and (4) 50% night ranges for each season (referred to as night ranges). Overall core ranges were calculated to understand vicuña day use in the area over the duration of the study, whether this space use differed between the Llano de los Leones and the San Guillermo Canyon sites, and to evaluate possible movement between these two areas during the study period. Seasonal home ranges, seasonal core ranges, and night ranges were calculated for two periods in each year based on plant phenology–the nongrowing period from June to November, and a growing period from

December to May (Donadio et al. 2012). For the day and night range estimation, the seasonal location data were separated into four categories according to the time of the day–dawn, day, dusk, and night–using the *sunriset* function in the maptools package in R (Bivand 2020). Since previous studies indicated daily movement occurred between day and night territories during dawn and dusk (Franklin 1974), we estimated seasonal core ranges and night ranges to identify important day and night areas after excluding points during dawn and dusk. Although rainfall in the park is largely limited to the months of January to March (Donadio et al. 2012), we included the months of December, April, and May in the growing period to ensure that home ranges were calculated for similar intervals and could be compared across these periods. Seasonal home ranges, seasonal core ranges, and night ranges were thus calculated for four distinct periods (nongrowing 2014, growing 2014, nongrowing 2015, and growing 2015) with data from 17, 13, 19, and 13 individuals, respectively. We did not conduct a seasonal analysis for the nongrowing 2016 and growing 2016 periods due to low sample sizes. The number of individuals varied across seasons due to multiple collaring phases and natural mortalities. We tested for the influence of resource availability on vicuña space use by calculating correlations between the seasonal core range size and mean Normalized Difference Vegetation Index (NDVI) and between seasonal core range size and family size. Mean NDVI values were calculated using google Earth Engine (Gorelick et al. 2017) from LANDSAT-8 imagery for each of the identified seasonal periods. For analyzing differences in home range sizes for the same vicuñas across seasons, we used the Friedman test (Friedman 1937).

Home range overlap: Seasonal core ranges were used for calculating overlap between vicuñas. The proportion of the seasonal core range of each vicuña individual that was shared with one or more other vicuñas from other families was calculated to determine exclusive-use areas and identify individuals that did not share home ranges. Next, we assessed whether overlap percentages changed across seasons for the same vicuñas, to understand if seasonal differences might be associated with patterns of range overlap. We used the Friedman test (Friedman 1937) to analyze differences in range overlap for the same vicuñas across seasons.

Diel migrations: To investigate the influence of resource availability and seasonality on diel migrations, we measured the distances moved by vicuñas between the centroids of the day and night areas on a daily basis. Wilcoxon ranked sum tests were used to analyze differences between daily distances moved in the two regions. Differences in daily distances moved between nongrowing and growing periods were analyzed using the Welch two-sample *t*-test.

Results

Vicuña family composition, group size, and site fidelity: Families with collared vicuñas included on average 3 (range 1–6) females and 2.1 (range 1–4) offspring. Visual inspection of plots generated by the *rhr* package offered evidence for site fidelity for all monitored individuals except one, where the result was inconclusive. The range shift test indicated no range shift for six vicuñas. For the remaining 18 vicuñas, although the range shift test was inconclusive, the largest 'migration distance' value of 0.043 km, with a range shift index value of 0.043, indicated that these vicuñas also did not shift ranges during the study. We did not find any movement between the two sites within the park (Fig. 1).

Home range size and variation in sizes: The mean (± *SD*) overall core range sizes from our study were 0.53 (± 0.81) km^2. Home range sizes using other methods and a comparison of home range sizes from previous studies are summarized in Table 1. Contrary to our predictions, we found little evidence for differences in range sizes between the Llano de los Leones and San Guillermo Canyon sites, regardless of type of home range examined (i.e., overall, seasonal, core; Supplementary Data SD2). One exception was for seasonal core ranges in the nongrowing period in 2014, where the average size of the seasonal core range for the San Guillermo Canyon (0.25 ± 0.10 km^2, $\bar{x}$ ± *SD*) was significantly higher (*P* = 0.04) than for the Llano de los Leones (0.11 ± 0.14 km^2, $\bar{x}$ ± *SD*). Seasonal core range sizes varied significantly across seasons (Friedman's chi-squared = 8.35, d.f. = 3, *P* = 0.04)–however, the effect size was small (Kendall's *W* = 0.253), and a post hoc Wilcoxon test with a Bonferroni correction resulted in no significant differences across pairs of seasons. Seasonal core range sizes did not vary significantly across seasons. We found no significant correlations between seasonal core range size and mean NDVI, except for the nongrowing 2015 period, when we found a significant but weak negative correlation. We also found weak, but not statistically significant, positive correlations between seasonal core range size and family size.
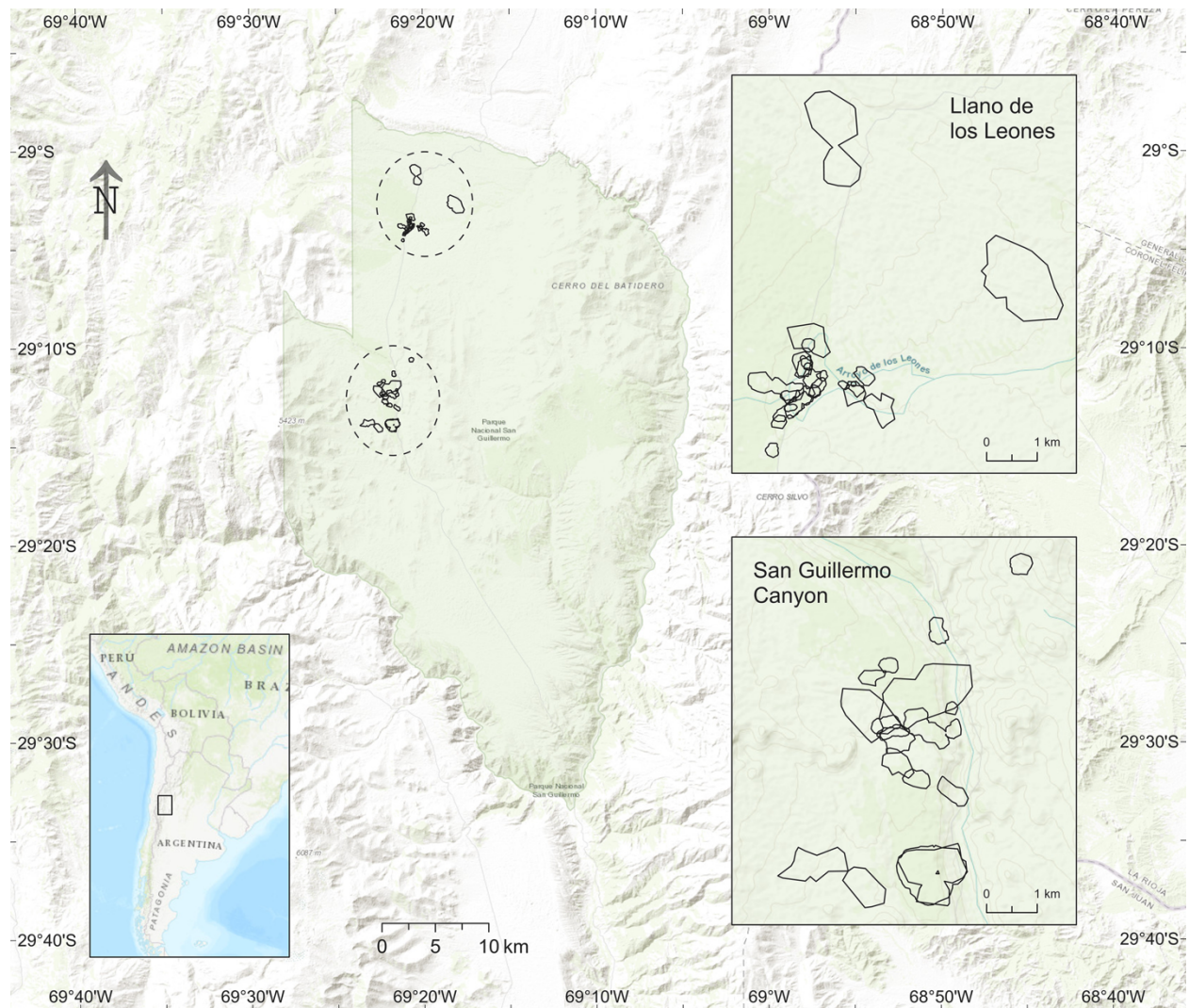
Figure 1: Vicuña core ranges in the Llano de los Leones (north) and the San Guillermo Canyon (south) areas in San Guillermo National Park for the duration of the study. No vicuña was observed to move between the two sites during the study period.

Range overlap: Vicuñas in San Guillermo National Park shared large portions (38.1 ± 37.38%, $\bar{x}$ ± *SD*) of their seasonal core ranges. We found support for our prediction that most vicuña seasonal core ranges overlap with those of other vicuñas–range sharing was high across measurement periods and sites in the park, whereby less than a fourth of the seasonal core ranges were exclusive (no portion shared with other vicuñas). Overlaps varied significantly across seasons (Friedman's chi-squared = 8.08, d.f. = 3, $P = 0.04$) - however, the effect size was small (Kendall's $W = 0.245$), and a post hoc Wilcoxon test with a Bonferroni correction resulted in no significant differences across pairs of seasons. In each seasonal analysis period, at least three and up to 10 vicuñas shared more than a third of their seasonal core ranges with other vicuñas.

Location	Method	Home range size (km²)	Reference
Huaylarco, Peru	MCP[a]	0.13[b]	Koford 1957

Pampas Galeras Reserve, Peru	MCP[a]	0.18	Franklin 1976
Pozuelos Biosphere Reserve, Argentina	KDE	0.19	Arzamendia et al. 2018
San Guillermo National Park, Argentina	aLoCoH	0.53	-
	AKDE	0.35	-
	MCP	2.42	-

[a] Equivalent to a Minimum Convex Polygon; however, home ranges were delineated manually using visual observations
[b] Median value reported. All other values are means.

Table 1.—A comparison of 50% home range sizes for vicuñas for the duration of the study in San Guillermo National Park using aLoCoH, AKDE and MCP with vicuña home range sizes reported in previous studies.

Diel migrations: Vicuña daily movement between day and night areas differed between the two sites and across seasons. Vicuñas in Llano de los Leones moved 822.4 m (95% confidence interval [*CI*] 810.9–833.9) on average during diel migrations between their day and night core areas, significantly more ($W = 62,007,750$, $P < 0.001$) than the 724.8 m (95% *CI* 708.9–740.6) average daily movement in the San Guillermo Canyon. Average daily distance moved between day and night areas also differed significantly ($t = -3.35$, $P = 0.001$) between the growing and nongrowing seasons, whereby the distance between day and night areas was on average 763.4 m (95% *CI* 748.3–778.5) in the growing season compared to 796.4 m (95% *CI* 784.3–808.4) in the nongrowing season. Vicuña individuals moved a total of 291.9 km (95% *CI* 260.9–322.9) annually, with a range of 145.5–440.3 km. Diel migration distances increased during the nongrowing period in the Llano de los Leones, peaking early in the growing period, as compared to the San Guillermo Canyon, where distances peak at the beginning of the nongrowing period and subsequently decline (Fig. 2). Night ranges were not clustered together with other vicuñas and differed in their relationship to seasonal core ranges between sites - vicuñas in the Llano de los Leones used distinct areas in the more open uplands (areas that represented lower predation risk), while those in the San Guillermo Canyon used higher-elevation areas of their day seasonal core ranges.
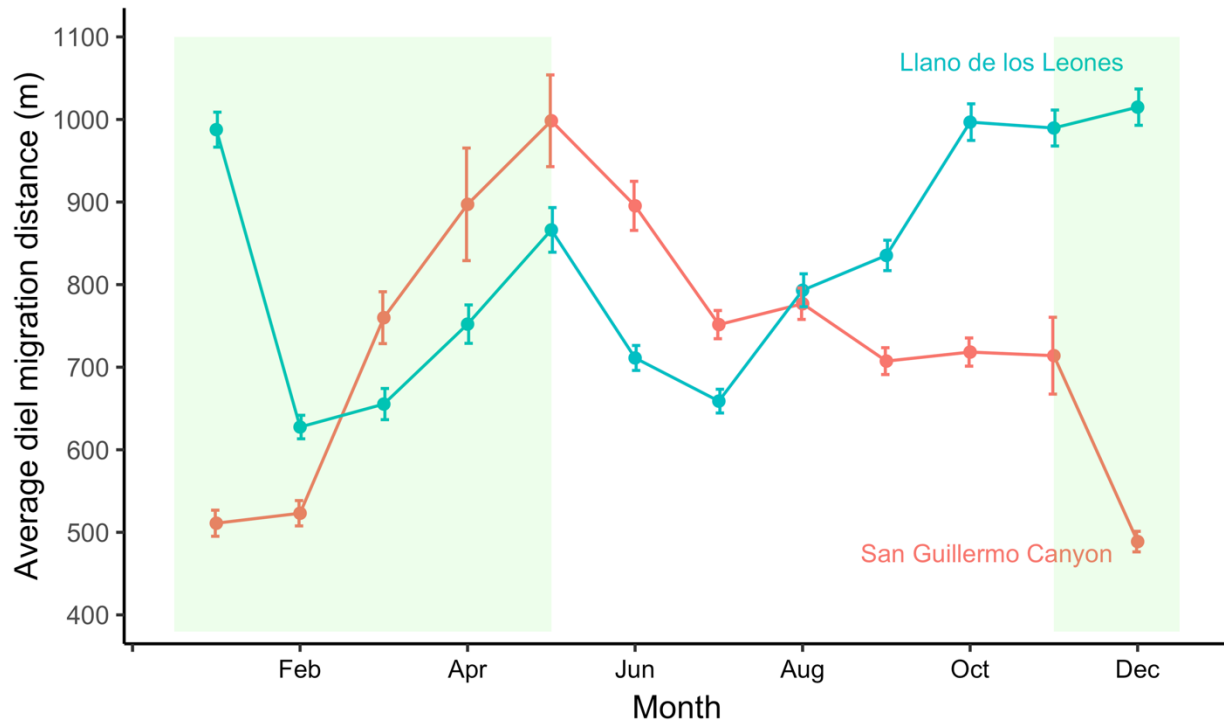
Figure 2: A comparison of diel migration distances calculated on a monthly basis for vicuñas in the Llano de los Leones and San Guillermo Canyon for the duration of the study. Diel migration distances increased during the non-growing period in the Llano de los Leones as compared to the San Guillermo Canyon where distances peak at the beginning of the non-growing period and subsequently decline. The bars represent 95% confidence intervals based on standard errors. The green shaded area represents the growing season.

Discussion

We studied vicuña spatial and social ecology using GPS location data in the southern end of its range in the Andes. Although some understanding of vicuña space use exists (Koford 1957; Franklin 1974, 1976; Arzamendia et al. 2018), previous studies are based on visual observations of marked animals, as opposed to GPS location data sets that allow for the ability to investigate animal space use and movement continuously across large temporal and spatial scales. Past research was also generally conducted in areas where vicuñas share landscapes with people to some degree, and in areas with relatively higher levels of precipitation (Koford 1957; Franklin 1976; Arzamendia et al. 2018). By contrast, the extremely remote location of our study site affords us a baseline picture of a species otherwise exposed to significant disturbance and threats elsewhere in its range. Additionally, the considerably lower levels of precipitation at our study site (Salvioli 2007) may affect space use and space sharing, offering an opportunity to gain insights on how space use in the species changes across environmental gradients.

Vicuñas in San Guillermo National Park were sedentary (i.e., did not undertake seasonal migrations) and demonstrated high site fidelity, in line with previous studies that observed year-round maintenance of territories by vicuña families (Franklin 1974, 1976; Bosch and Svendsen 1987). Collared vicuñas did not move between Llano de los Leones and San guillermo Canyon, the two sites examined within the park. The home range estimates from our study were more

than twice as large as previously reported (Table 1; Koford 1957; Franklin 1976; Arzamendia et al. 2018). We contend that the differences in range sizes could be a result of other studies being conducted in areas with higher precipitation levels and therefore higher primary productivity. For instance, the Pozuelos Biosphere Reserve in Argentina receives 46% more annual precipitation than San Guillermo National Park (Arzamendia et al. 2018). Koford (1957) suggested that vicuñas may use much larger territories, up to 1.01 km^2, in barren parts of their range. Our results are also in line with space use predictions under the resource dispersion hypothesis, which suggests that clumped resources are likely to increase territory size (Macdonald 1983; Johnson et al. 2002). While this is a possibility, the differences in home range size could also result from methodological differences, since estimates from previous studies were based on a visual estimation of movements in the landscape rather than using quantitative home range estimation methods based on systematic data collection over sustained periods of time, as is possible with GPS collar data. Studies based on data obtained through visual observations have limitations in terms of obtaining a sufficient number of locations for determining accurate home ranges, with the data likely not meeting asymptotic requirements (Laver and Kelly 2008).

Vicuña seasonal core ranges were similar in size across the two sites in the park, despite the differences in NDVI, elevation, and slope between the Llano de los Leones and the San Guillermo Canyon, and the fact that NDVI acts as a spatial anchor for vicuñas (very limited habitat where vicuñas are drawn to due to high forage availability; Smith et al. 2019b). One exception occurred in the nongrowing period in 2014, when seasonal core ranges in the San Guillermo Canyon were more than twice as large as those in the Llano de los Leones, a result at odds with recent research that offers strong support for the habitat productivity hypothesis (Seigle-Ferrand et al. 2021). However, given the fact that neither seasonal home range nor seasonal core range sizes significantly change across analysis periods, we ascribe the difference in the core ranges to the inherent stochasticity associated with space use. Despite differences in plant phenology in the study area across the growing and nongrowing periods, seasonal core range sizes did not change across these periods, contrary to observations from previous studies that reported seasonal changes in territory size (Koford 1957). The absence of seasonal variation in seasonal core range size aligns with the very weak relationships observed between seasonal core range size and mean NDVI and seasonal core range size and family group size, also at odds with previously reported observations for the species (Franklin 1976; Arzamendia et al. 2018). In contrast with previous studies, we found considerable evidence for tolerance of conspecifics from different families, especially while foraging (Franklin 1974, 1976)–most vicuña seasonal core ranges in San Guillermo National Park overlapped with seasonal core ranges of other individuals, with very few exclusive core ranges. This was corroborated by visual observations recorded opportunistically during the study period that revealed as many as five collared vicuñas from distinct family groups feeding in close proximity to each other on multiple occasions. Except for a few individuals, space sharing varied across seasons, seemingly in a stochastic manner - we did not detect systematic differences in seasonal core range overlap between the four seasons, despite earlier studies reporting increased territorial behavior during the breeding and birthing periods (Franklin 1976). Instead, we observed significant continuity of seasonal core ranges within individuals and considerable variation in proportions of seasonal core ranges shared with other sampled individuals (i.e., range overlap), which may suggest personality differences in terms of varying levels of aggression and repulsion behavior displayed by males in the same population (Franklin 1974). We conclude that vicuñas in the park deviate from the

behavior of strictly exclusive-use territories described in some previous studies on this species (Koford 1957; Franklin 1974; Arzamendia et al. 2018; but see Vilá and Roig 1992; Vilá 1994; Cassini et al. 2009) in line with the predictions of the resource dispersion hypothesis (Macdonald 1983; Johnson et al. 2002). The results reported by Arzamendia et al. (2018) are especially comparable with our study, given the use of a quantitative method for home range estimation and that both studies were conducted on the southern vicuña subspecies, *L. v. vicugna*. At the same time, we acknowledge the limitations of comparing our results with those from Koford (1957) and Franklin (1974), given that territoriality and territories are largely behavioral concepts that are difficult to test based on purely remotely obtained data, as opposed to home ranges that can be reasonably derived from biologging animal location data.

Vicuña families in the park did not maintain clustered communal night ranges, instead largely choosing to use smaller areas within their seasonal home ranges or other areas in the open uplands. While vicuñas in both sites moved to higher-elevation areas for the night (Supplementary Data SD3), the flatter, less rugged terrain in the Llano de los Leones possibly results in vicuñas moving longer distances to reach their preferred night areas. Another possible factor may be that vicuñas in the Llano de los Leones may prefer to move farther away from the day foraging sites due to the high predation risk associated with the day sites (Smith et al. 2019a). However, given that vicuñas do not use some of the even-higher areas within the park, it is likely that elevation is one of several factors that vicuñas use to select refuge sites.

Although vicuñas in San Guillermo National Park did not migrate on a seasonal basis and maintained year-round home ranges, they undertook diel migrations, moving from the highly productive high-quality forage areas often located at relatively lower altitudes to the low productive open plains located at high altitudes. With the open plains in the park representing safe areas with low predation risk (Smith 2019a), vicuñas use diel migrations as an antipredator strategy in San Guillermo National Park (Smith 2019a). Diel migrations have been well-studied in marine environments (Neilson and Perry 1990; Alonzo et al. 2003; Hays 2003); however, their understanding in terrestrial systems is limited to a few species, such as plains zebras (*Equus quagga*; Courbin et al. 2019). Although vicuñas moved significantly longer average daily distances during the nongrowing period, the biological significance of this is likely to be limited due to the small difference across seasons. The differences in daily distances at the monthly level (Fig. 2), however, offer insights into the impacts of seasonal effects and differences in terrain at the two sites in the park. Vicuña daily distances reduced at the beginning of the growing season, likely due to the increased availability of forage, with reductions of 32% and 36%, respectively, in San Guillermo Canyon and Llano de los Leones. The decrease in daily distances in San Guillermo Canyon during the nongrowing season could be a strategy to save energy, when forage is limited and less nutritious. A more complex trade-off between managing predation risk, conserving energy, and achieving access to forage may explain the initial drop followed by a steady increase in daily distances in the nongrowing season in the Llano de los Leones, which comprises concentrated sources of vegetation in the low-lying areas, surrounded by plains. These daily movements, although not as dramatic or landscape-altering as long-distance seasonal migrations, may, however, be important due to the likely significant energetic costs involved. With increasing options for including energetics assessments in GPS collars, we propose that future work on the species assesses the energetic impacts of these daily migrations and compare them with long-distance seasonal migrations. Studies on vicuña populations in areas where large

predators are functionally extinct and where the species does not face hunting pressures may also offer additional insights on this behavior.

Our analysis found several key differences with previous studies in vicuña behavior and space. Vicuña home ranges in San Guillermo were considerably larger than in previous estimates. Overlaps between home ranges were common, with most vicuñas sharing large portions of their home range with other individuals. Vicuña home range sizes did not undergo seasonal changes and did not vary with changing family sizes and availability of vegetation in the home range. Our work highlights the differences in behavior likely arising from a combination of environmental factors and the fact that the San Guillermo National Park vicuña populations are almost completely undisturbed by human activity. From a broader perspective, this study offers an insight into the plasticity of social behavior and tolerance of nonfamilial conspecifics in the species. In semiarid areas like San Guillermo National Park with plant growth occurring only during a short growing season, the limited availability of forage may preclude territorial behavior in feeding areas and increase tolerance of nonfamilial conspecifics during the day. Similar breakdowns in territorial behavior and increased tolerance of conspecifics when food availability is limited or concentrated in small geographical areas have been demonstrated in other mammalian (Newsome et al. 2013) and avian (Carpenter and MacMillen 1976) species. The flexibility in social behavior and space use displayed by the species may be instrumental in ensuring survival, and its recent resurgence, in this extremely arid and harsh landscape.

Acknowledgments

References

Acebes, P., Wheeler, J., Baldo, J., Tuppia, P., Lichtenstein, G., Hoces, D., & Franklin, W. L. (2018). *Vicugna vicugna* (errata version published in 2019). The IUCN Red List of Threatened Species. 2018; e. T22956A145360542.

Alonzo, S. H., Switzer, P. V., & Mangel, M. (2003). Ecological games in space and time: the distribution and abundance of Antarctic krill and penguins. *Ecology*, *84*(6), 1598-1607.

Arzamendia, Y., Carbajo, A. E., & Vilá, B. (2018). Social group dynamics and composition of managed wild vicuñas (Vicugna vicugna vicugna) in Jujuy, Argentina. *Journal of Ethology*, *36*(2), 125-134.

Bivand, R.. Lewin-Koh, N. (2020). maptools: Tools for handling spatial objects. *R Package Version 1.0-2*.

Bonacic, C., & Galaz, J. L. (2001). Conservación y manejo de la vicuña en Chile. In J. L. Galaz, G. Gonzalez (eds), *Proceedings of I Seminario Internacional Aprovechamiento de la fibra de vicuña en los Andes de Argentina, Bolivia, Chile y Perú, Arica, Chile. Conservación y manejo de vicuñas en Sudamérica (pp. 121-133).*

Bonacic, C., & Gimpel, J. (2003). Sustainable use of the vicuña: a critical analysis and the MACS project. *Conserving biodiversity in arid regions: best practices in developing nations*, 345-354.

Bonacic, C., & Macdonald, D. W. (2003). The physiological impact of wool-harvesting procedures in vicunas (*Vicugna vicugna*). *Animal Welfare*, *12*(3), 387-402.

Bosch, P. C., & Svendsen, G. E. (1987). Behavior of male and female vicuna (*Vicugna vicugna* Molina 1782) as it relates to reproductive effort. *Journal of mammalogy*, *68*(2), 425-429.

Carpenter, F. L., & MacMillen, R. E. (1976). Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science*, *194*(4265), 639-642.

Cassini, M., Borgnia, M., Arzamendia, Y., Benítez, V., & Vilá, B. (2009). Sociality, foraging and habitat use by vicuña. *The Vicuña: The Theory and Practice of Community Based Wildlife Management*, 35-48.

Courbin, N., Loveridge, A. J., Fritz, H., Macdonald, D. W., Patin, R., Valeix, M., & Chamaillé-Jammes, S. (2019). Zebra diel migrations reduce encounter risk with lions at night. *Journal of Animal Ecology*, *88*(1), 92-101.

Donadio, E., & Buskirk, S. W. (2006). Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. *Biological Conservation*, *127*(2), 139-145.

Donadio, E., Novaro, A. J., Buskirk, S. W., Wurstten, A., Vitali, M. S., & Monteverde, M. J. (2010). Evaluating a potentially strong trophic interaction: pumas and wild camelids in protected areas of Argentina. *Journal of Zoology*, *280*(1), 33-40.

Donadio, E., Buskirk, S. W., & Novaro, A. J. (2012). Juvenile and adult mortality patterns in a vicuña (Vicugna vicugna) population. *Journal of Mammalogy*, *93*(6), 1536-1544.

Donadio, E., & Buskirk, S. W. (2016). Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. *Journal of Mammalogy*, *97*(3), 966-977.

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., & Calabrese, J. M. (2015). Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology*, *96*(5), 1182-1188.

Fletcher, R., & Fortin, M. (2018). *Spatial ecology and conservation modeling* (p. 523). Cham: Springer International Publishing.

Franklin, W. L., (1974). The social behavior of the vicuña. In V. Geist, F. Walter (eds), *Proceedings of an international symposium, 2-5 Nov 1971; University of Calgary, Alberta, Canada. The behaviour of ungulates and its relation to management. Vol 1 (pp. 477-487).* International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

Franklin, W. L. (1978). *Socioecology of the Vicuña*. Utah State University, Logan, Utah, USA

Friedman, M. (1937). The use of ranks to avoid the assumption of normality implicit in the analysis of variance. *Journal of the american statistical association*, *32*(200), 675-701.

Getz, W. M., & Wilmers, C. C. (2004). A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography*, *27*(4), 489-505.

Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J., & Wilmers, C. C. (2007). LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. *PloS one*, *2*(2), e207.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote sensing of Environment*, *202*, 18-27.

Gurarie, E., & Cheraghi, F. (2017). marcher: migration and range change estimation in R. R package version 0.0-2.

Gurarie, E., Cagnacci, F., Peters, W., Fleming, C. H., Calabrese, J. M., Mueller, T., & Fagan, W. F. (2017). A framework for modelling range shifts and migrations: asking when, whither, whether and will it return. *Journal of Animal Ecology*, *86*(4), 943-959.

Harestad, A. S., & Bunnel, F. L. (1979). Home range and body weight--A reevaluation. *Ecology*, *60*(2), 389-402.

Hays, G. C., (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, *503*, 163-170.

Johnson, D. D., Kays, R., Blackwell, P. G., & Macdonald, D. W. (2002). Does the resource dispersion hypothesis explain group living?. *Trends in ecology & evolution*, *17*(12), 563-570.

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478.

Koford, C. B. (1957). The vicuña and the puna. *Ecological monographs*, *27*(2), 153-219.

Laver, P. N., & Kelly, M. J. (2008). A critical review of home range studies. *The Journal of Wildlife Management*, *72*(1), 290-298.

Lichtenstein, G. (2009). Vicuña conservation and poverty alleviation? Andean communities and international fibre markets. *International Journal of the Commons*, *4*(1).

Lott, D. F. (1991). Intraspecific Variation in the social systems of Wild Vertebrates. Vol. 2. Cambridge University Press Cambridge.

Macdonald, D. W. (1983). The ecology of carnivore social behaviour. *Nature*, *301*, 379-384.

Maher, C. R., & Lott, D. F. (2000). A review of ecological determinants of territoriality within vertebrate species. *The American Midland Naturalist*, *143*(1), 1-29.

McLaren, B. E., MacNearney, D., & Siavichay, C. A. (2018). Livestock and the functional habitat of vicuñas in Ecuador: a new puzzle. *Ecosphere*, *9*(1), e02066.

McNeill, D., Gabriela, L., & Nadine, R. D. A. (2009). International policies and national legislation concerning vicuna conservation and exploitation. In I. J. Gordon, (ed), *The vicuña: the theory and practice of community based wildlife management*, *Springer, Boston, USA (pp. 63-79).*

Menard, N. (1982). Some aspects of the socioecology of the vicuna Lama vicugna Molina. *Revue d'Ecologie*, *36*, 15-35.

Monk, J. D., Smith, J. A., Donadío, E., Perrig, P. L., Crego, R. D., Fileni, M., Bidder, O., Lambertucci, S. A., Pauli, J. N., Schmitz, O. J., & Middleton, A. D. (2022). Cascading effects of a disease outbreak in a remote protected area. *Ecology Letters*, *25*(5), 1152-1163.

Munger, J. C. (1984). Home ranges of horned lizards (Phrynosoma): circumscribed and exclusive? *Oecologia*, *62*, 351-360.

Neilson, J. D., & Perry, R. I. (1990). Diel vertical migrations of marine fishes: an obligate or facultative process? *Advances in marine biology*, *26*, 115-168.

Newsome, T. M., Ballard, G. A., Dickman, C. R., Fleming, P. J., & van de Ven, R. (2013). Home range, activity and sociality of a top predator, the dingo: a test of the Resource Dispersion Hypothesis. *Ecography*, *36*(8), 914-925.

Owen-Smith, N. (1977). On territoriality in ungulates and an evolutionary model. *The Quarterly Review of Biology*, *52*(1), 1-38.

Perrig, P. L., Donadio, E., Middleton, A. D., & Pauli, J. N. (2017). Puma predation subsidizes an obligate scavenger in the high Andes. *Journal of Applied Ecology*, *54*(3), 846-853.

Puig, S., & Videla, F. (2007). Distribución, densidades y estado de conservación de los camélidos. In E. Martínez Carretero, (ed), *Diversidad Biológica y Cultural de los Altos Andes Centrales de Argentina - Línea de base de la Reserva de Biosfera San Guillermo, San Juan. Fundación Universidad Nacional de San Juan, San Juan, Argentina (pp. 197-223).*

Ryan, S. J., Knechtel, C. U., & Getz, W. M. (2006). Range and habitat selection of African buffalo in South Africa. *The Journal of Wildlife Management*, *70*(3), 764-776.

Salvioli, G. (2007). Caracterización hidrometeorológica. In E. Martínez Carretero, (ed), *Diversidad biológica y cultural de los Altos Andes Centrales de la Argentina: línea de base de la reserva de la biosfera San Guillermo (pp. 63-87).*

Seigle-Ferrand, J., Atmeh, K., Gaillard, J. M., Ronget, V., Morellet, N., Garel, M., Loison, A., & Yannic, G. (2021). A Systematic Review of Within-Population Variation in the Size of Home Range Across Ungulates: What Do We Know After 50 Years of Telemetry Studies? *Frontiers in Ecology and Evolution*, *8*, 555429.

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., & Middleton, A. D. (2019). Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places. *Oecologia*, *189*, 883-890.

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., Bidder, O. R., & Middleton, A. D. (2019). Habitat complexity mediates the predator–prey space race. *Ecology*, *100*(7), e02724.

Signer, J., & Balkenhol, N. (2015). Reproducible home ranges (rhr): A new, user-friendly R package for analyses of wildlife telemetry data. *Wildlife Society Bulletin*, *39*(2), 358-363.

Sikes, R. S., Gannon, W. L., & Animal Care and Use Committee of the American Society of Mammalogists. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of mammalogy*, *92*(1), 235-253.

Spencer, S. R., Cameron, G. N., & Swihart, R. K. (1990). Operationally defining home range: temporal dependence exhibited by hispid cotton rats. *Ecology*, *71*(5), 1817-1822.

Vilá, B. L., & Roig, V. G. (1992). Diurnal movements, family groups and alertness of vicuña (Vicugna vicugna) during the late dry season in the Laguna Blanca Reserve (Catamarca, Argentina). *Small Ruminant Research*, *7*(4), 289-297.

Vila, B. L. (1994). Use of dung piles by neighbouring vicuñas. *Zeitschrift fur Saugetierkunde, 59*(2), 126.

Vilá, B. L. (2000). Comportamiento y organización social de la vicuña. In B. González, F. Bas, C. Tala, A. Iriarte, (eds), *Proceedings of the International Seminar on Manejo sustentable de la vicuña y el guanaco; Servicios Agrarios y Ganaderos de la Universidad C, Católica de Chile, Santiago de Chile, Chile. (pp. 175-191).*

Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, *96*(7), 1741-1753.

Supplementary Data

Supplementary Data SD1: Total number of GPS locations recorded with start and end dates and number of months with data for each vicuña in San Guillermo National Park.

Vicuña ID	Total number of locations	Start date	End date	Number of months with data
		Llano de los Leones		
14	946	03 May 2014	29 Aug 2014	4
16	7675	10 May 2014	24 Dec 2016	32
17	1127	15 May 2014	03 Oct 2014	5
18	4221	27 May 2015	05 Nov 2016	17
23	5832	01 Jun 2014	30 May 2016	24
24	6232	09 May 2014	25 Jun 2016	25
25	7741	07 May 2014	30 Dec 2016	32
27	1294	16 May 2014	25 Oct 2014	5
30	5690	07 May 2014	18 Apr 2016	23
33	1700	08 Jun 2015	07 Jan 2016	7
34	8085	12 May 2014	16 Feb 2017	33
35	5995	05 May 2014	24 May 2016	25
36	2884	16 May 2014	12 May 2015	12
		San Guillermo Canyon		
13	5259	08 Jun 2014	27 Mar 2016	22
15	1165	11 Jun 2015	03 Nov 2015	5
19	4381	01 May 2014	31 Oct 2015	18
20	6124	07 Jun 2014	12 July 2016	25
21	2565	17 May 2015	01 April 2016	11
22	5551	06 Jun 2014	29 Apr 2016	23
26	1257	07 June 2015	11 Nov 2015	5
28	1970	29 May 2015	30 Jan 2016	8
29	5595	10 May 2014	08 Apr 2016	23
31	1062	11 May 2015	20 Sep 2015	4
32	1521	30 April 2014	06 Nov 2014	7

Supplementary Data SD2: Vicuña home range sizes in the two sites in San Guillermo National Park for different periods during the study: (a) overall core range sizes (km^2) from April 2014 to February 2017, (b) seasonal home and seasonal core ranges in km^2 for the 2014 nongrowing period, (c) seasonal home and seasonal core ranges in km^2 for the 2014 growing period, (d) seasonal home and seasonal core ranges in km^2 for the 2015 nongrowing period, and (e) seasonal home and seasonal core ranges in km^2 for the 2015 growing period.

Llano de los Leones		San Guillermo Canyon	
Individual id	**Overall core range (50%)**	**Individual id**	**Overall core range (50%)**
14	0.25	13	0.14

16	0.04	15	0.41
17	0.03	19	0.23
18	0.24	20	0.47
23	0.50	21	0.37
24	0.03	22	0.12
25	0.05	26	2.02
27	0.24	28	0.16
30	0.17	29	1.18
33	3.30	31	2.05
34	0.14	32	0.14
35	0.03		
36	0.37		

Vicuña ID	Seasonal home range (95%)		Seasonal core range (50%)	
	Day	Night	Day	Night
Llano de los Leones				
14	1.67	0.70	0.21	0.02
16	0.65	0.91	0.01	0.02
17	2.43	3.71	0.03	0.15
23	0.39	0.40	0.01	0.03
24	0.32	0.73	0.02	0.01
25	1.54	1.34	0.01	0.02
27	3.84	2.85	0.23	0.36
30	4.57	5.33	0.39	0.51
34	2.03	1.03	0.02	0.04
35	0.44	1.15	0.01	0.01
36	7.11	3.98	0.29	0.30
San Guillermo Canyon				
13	2.51	0.42	0.15	0.02
19	1.92	1.13	0.29	0.07
20	1.72	0.71	0.23	0.04
22	3.41	0.46	0.36	0.02
29	6.33	1.81	0.35	0.05
32	5.24	4.20	0.14	0.14

Vicuña ID	Seasonal home range (95%)		Seasonal core range (50%)	
	Day	Night	Day	Night
Llano de los Leones				
16	1.52	0.54	0.06	0.01
23	13.74	3.93	0.41	0.09
24	0.29	0.22	0.03	0.01
25	5.19	2.96	0.10	0.33
30	7.41	2.07	0.02	0.21
34	7.54	3.38	0.33	0.82
35	1.94	1.73	0.01	0.12

36	13.91	7.14	0.36	0.38
San Guillermo Canyon				
13	2.89	0.29	0.11	0.02
19	3.95	1.19	0.11	0.05
20	3.64	1.49	0.33	0.10
22	1.61	0.27	0.07	0.02
29	34.79	18.15	0.33	0.07

Vicuña ID	Seasonal home range (95%)		Seasonal core range (50%)	
	Day	Night	Day	Night
Llano de los Leones				
16	0.88	0.61	0.02	0.01
18	9.07	5.86	0.22	0.10
23	22.63	18.36	2.37	0.12
24	0.82	0.64	0.02	0.01
25	1.65	1.71	0.01	0.21
30	3.81	3.22	0.01	0.20
33	18.95	8.47	2.28	0.88
34	3.17	2.71	0.01	0.47
35	4.74	1.69	0.04	0.12
San Guillermo Canyon				
13	7.64	2.57	0.23	0.02
15	3.64	1.09	0.38	0.05
19	5.16	3.08	0.25	0.09
20	2.83	2.35	0.52	0.19
21	9.28	2.63	0.56	0.12
22	3.30	1.16	0.19	0.01
26	12.28	3.07	2.02	0.50
28	3.43	2.49	0.36	0.25
29	37.57	16.16	1.64	0.41
31	14.46	3.59	3.08	1.07

Vicuña ID	Seasonal home range (95%)		Seasonal core range (50%)	
	Day	Night	Day	Night
Llano de los Leones				
16	0.89	0.20	0.02	0.01
18	2.78	2.23	0.18	0.12
23	12.20	2.63	1.02	0.14
24	0.57	0.31	0.06	0.02
25	4.64	4.12	0.12	0.11
30	5.44	5.82	0.36	0.49
34	2.58	1.55	0.07	0.05
35	1.40	1.54	0.01	0.04

San Guillermo Canyon				
13	1.68	0.57	0.06	0.02
20	6.77	1.91	0.41	0.38
21	1.14	0.45	0.19	0.03
22	1.76	0.25	0.09	0.02
29	2.58	0.71	0.47	0.13

Supplementary Data SD3: Centroids of day (triangles) and night (circles) locations of vicuñas in the (a) Llano de los Leones and (b) San Guillermo Canyon in San Guillermo National Park. Map scales differ for (a) and (b). All vicuñas except one in the San Guillermo Canyon moved to higher locations for the night.
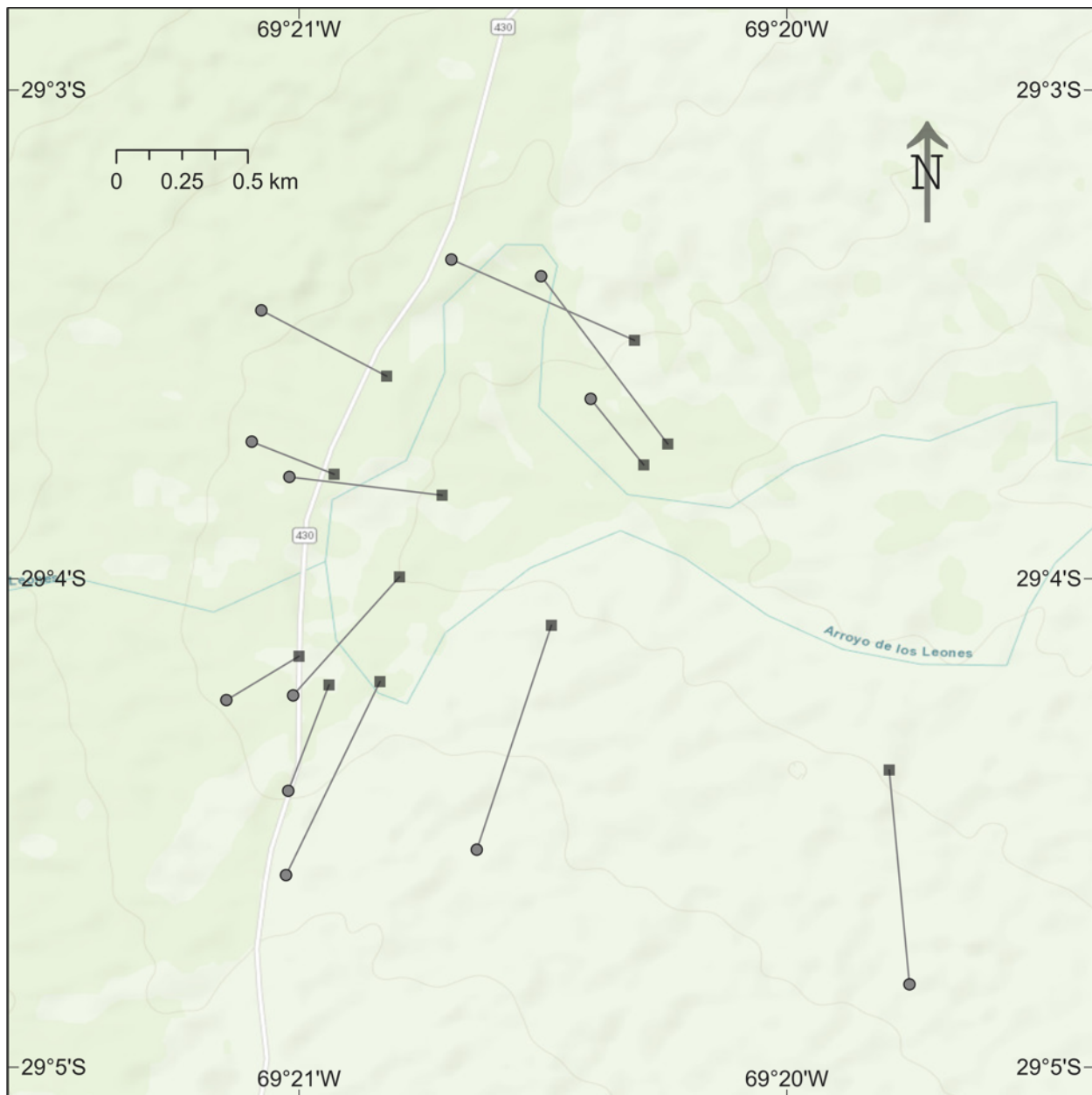
The previous chapter looked at an animal's use of space and movement within a protected area. These analyses offer important insights into how a species may behave in a specific knowledge part of its range and offers us the opportunity to compare this understanding with previous of the species. In the next chapter, I assess how a species uses space and moves across different parts of its range, and how this space use may be driven by environmental factors.

Chapter 2: The role of landscape heterogeneity and structure in space use of a wide-ranging large carnivore

Abstract

Environmental conditions and landscape factors can have dramatic impacts on animal space use patterns and behavior. We investigated the impact of landscape heterogeneity and structure on space use and predation behavior of a large terrestrial predator, the puma, across three sites in the Patagonian and the high Andean steppes. Pumas at our sites demonstrated considerable flexibility in their behavior and space use, behaving more similarly to the archetypical ambush hunter in the high Andes, but displaying traits closer to coursing predators in the sites in the Patagonian steppe. We also found that puma predation sites were more clustered compared to all used locations, suggesting that pumas use limited areas within their home ranges while hunting primary prey, in line with behavior expected from an ambush hunter. Puma space use was highly clustered in landscapes with low heterogeneity. However, the impact of landscape complexity and variability on overall puma space use and the spatial distribution of kill sites is highly contextual, and our results suggest that, while typically understood as ambush hunters, pumas are versatile predators that display considerable plasticity in space use and hunting behavior.

Introduction

Large carnivores are deemed to play important roles in ecosystem functioning (Allen et al. 2017) but have seen significant population declines and range contractions across the world over the past century (Wolf and Ripple 2017). Understanding large carnivore space use, predation patterns and behavior is critical for developing effective conservation measures for the long-term persistence of many of these species, but a systematic understanding of these factors is challenging, in part, due to the tremendous flexibility that these organisms display - many large carnivores exhibit significant cognitive and behavioral complexity and interact with prey across diverse landscapes, where predation strategies and broader space use strategies could be modified. While significant progress has been made in recent years in understanding the landscape of fear and risk of predation from the perspective of prey (Laundre et al. 2001; Gaynor et al. 2019; Smith et al. 2019a), how predators perceive and use the landscape (in this case, the landscape of opportunity) is unclear.

Predators can be broadly categorized into three types (McLaughlin 1989; Schmitz 2005): (1) sit-and-wait or ambush predators that tend to wait for long periods of time in a particular location, with limited rapid movements during the attack, (2) sit-and-pursue predators that are similar to ambush predators, but typically chase their prey for longer distances before subduing it, and (3) active hunting or coursing predators that continuously move across the landscape and chase and attack prey whenever and wherever a feasible pursuit presents itself. These different hunting modes can affect prey behavior and landscapes (Schmitz et al. 2008) through direct, consumptive effects and indirect, non-consumptive effects (Coen et al. 1981; Preisser et al. 2007; Michel and

Adams 2009); however, the reverse, i.e., the impact of landscape heterogeneity on large carnivore behavior and space use is not well understood.

The puma (*Puma concolor*) has the largest latitudinal range of any terrestrial mammal, which makes the species an important model for examining the influences of environmental factors on hunting behavior and the predation risk landscape. Pumas thrive in a wide variety of habitats across the Americas and display considerable dietary flexibility across their range (Karandikar et al. 2022). Although the puma is commonly known as an ambush hunter (Murphy et al. 1998; Ruth and Murphy 2009), and thus expected to restrict predation to specific areas within the landscape that facilitate this hunting strategy, this assumption has not been rigorously tested. Most carnivore predation habitat selection studies focus on the narrow range of habitat features defining the location of a kill or other activity, i.e., third-order selection (Johnson 1980). Previous puma habitat selection studies, for example, have reported that pumas tend to select for sites in relatively low elevation areas with rugged terrain and specific vegetation classes, and that selection differs across sites (Blake and Gese 2016; Cristescu et al. 2019; Smith et al. 2019a). Little is known, however, about whether the distribution of kill sites varies with landscape heterogeneity. While previous research suggests that structural complexity may affect hunting behaviors in some taxa (Michel and Adams 2009), this has not been tested for pumas or other large carnivores.

In this project, we aim to evaluate the spatial distribution of puma space use patterns across three sites in the Patagonian steppe and the high Andes, with emphasis on the influence of environmental factors and landscape conditions on these patterns. First, we hypothesize that as ambush predators, pumas use limited areas of their home range while hunting and predict that puma predation sites for primary prey are more clumped than non-kill locations. Second, we hypothesize that landscape heterogeneity and structure (explained below) affect puma space use and predict that (a) decreasing landscape heterogeneity constrains overall puma space use within the home range, (b) puma predation sites are more clustered with decreasing landscape heterogeneity in the home range and (c) puma predation sites are more clustered with decreasing landscape productivity. Monk and Schmitz (2022) hypothesize that predation risk may be more clustered in landscapes with low productivity. Next, we hypothesize that landscape heterogeneity affects puma daily movement rates and predict that puma daily movements increase with increasing heterogeneity in the landscape. To address these hypotheses, we compared clusteredness of all-use locations and primary prey predation sites within and across the three sites, and mean daily distances moved across the three sites.

Methods

Study systems: Our study areas were located in three parks in Argentina: San Guillermo National Park, San Juan Province; Patagonia Park, Santa Cruz Province; and Monte Leon National Park, Santa Cruz Province. San Guillermo National Park (subsequently referred to as San Guillermo) is located in a remote part of the Central Andes mountains, occurring at an altitude of 2000-5600 meters above sea level (Donadio and Buskirk 2016) and receives 100-500 mm of precipitation annually, mostly during the summer months of January to March (Salvioli 2007). Most of San Guillermo comprises medium-altitude plains with small meadows (approximately 1.5% of the total area) and steep canyons (Smith et al. 2019b). Vegetation is most prevalent in the meadows in the form of tall grasses, but shrubs are also common in canyon habitats, defined as areas with

significant topographic variation. Patagonia Park is a recently created private park in the Patagonian steppe adjacent to the Andes. The park lies at an elevation of 200-1600 meters and consists of characteristic steppe grasslands interspersed with several canyons (Candino et al. 2022). Average annual precipitation levels in the area are 100-250 mm (Candino et al. 2022). Monte Leon National Park (subsequently referred to as Monte Leon), a protected area created in 2004, is located on the Atlantic coast of Argentina. The park lies at an elevation of 0-350 meters and receives 250 mm of precipitation annually, largely during the winter months of May to August (Barros et al. 1979). Monte Leon consists of typical steppe grassland habitat interspersed with small canyons that open out into sandstone cliffs and small beaches that line the coastline. Pumas are the apex predators and the only large predator at all the three sites. Vicuñas (*Vicugna vicugna*) are the most common large ungulate prey in San Guillermo (Donadio et al. 2012) and guanacos (*Lama guanicoe*) are found in low densities (Puig and Videla 2007), with vicuñas ten times as prevalent as guanacos in the system (Donadio and Buskirk 2016) at the time of data collection. Guanacos are the only large ungulate species in Patagonia Park and Monte Leon. Monte Leon also hosts a large nesting colony of magellanic penguins (*Spheniscus magellanicus*) that typically utilize the site from September to April, with the species representing a substantial marine food subsidy to pumas in the region (Serota et al. 2023).

Puma location data: We used GPS collars (Iridium Track M2D, Lotek at San Guillermo and LiteTrack Iridium 420, Lotek at Patagonia Park and Monte Leon) to obtain locations used by pumas at each site. Pumas were captured using leg traps and subsequently sedated using Ketamine (2mg/kg) with Xylazine (2mg/kg) under permits #DCM 455 and #DRPA 162 issued by the Administración de Parques Nacionales, Argentina, for San Guillermo and Monte Leon respectively. For Patagonia Park, permits were issued by the Wildlife Agency for Santa Cruz province. Pumas were collared at the start of the study and subsequently when previously used collars became available due to the death of collared individuals; as a result, the number of active collared individuals at each site varied throughout the duration of the study. Collars were programmed to obtain GPS fixes at varying frequencies ranging from 10 minutes to 3 hours; the obtained data were subsequently rarified to 1 fix per every 3 hours for our analysis. Previous work suggests that puma kills can be accurately identified with location data with a 3-hour fix, even with missing locations due to acquisition failure (Knopff et al. 2010). Puma location data was obtained between 2014 to 2017 at San Guillermo, and between 2019-2022 in Patagonia Park and Monte Leon.

Identification and investigation of likely predation sites: Clusters were defined as a group of two or more GPS locations for the same puma that were located within 20 meters of each other in a period of 36 hours; these criteria have been used previously for studies of puma predation and behavior in San Guillermo (Smith et al. 2020). A subset of clusters were investigated by field teams by visiting the cluster locations and conducting systematic searches to identify kill sites and record data associated with the predation event, if applicable. Several challenges prevented cluster investigations from being conducted across all seasons in the year or at systematic intervals, including the extremely remote location and high costs involved for conducting field work in San Guillermo, the difficulties involved in winter access and the limitations imposed by the COVID-19 pandemic during the study period in Patagonia Park and Monte Leon. To overcome the potential spatial and temporal biases associated with investigating clusters periodically and to use data from periods during which clusters investigations could not be conducted, we developed separate kill prediction models for each site to determine the

probability of a cluster being a primary prey kill site, using the caret package in R (Kuhn 2008) and a 4-step methodology. First, we developed logistic regression, random forest and gradient-boosted machine models comprising key cluster-related variables and landscape factors and compared these models, primarily using kappa as an indicator of model performance. Random forest and gradient-boosted machine models are machine learning algorithms that are well-suited for classification problems. For all the three sites, the random forest models outperformed the logistic regression and gradient-boosted machine models. Second, we used the 'rfe' function in the caret package in R (Kuhn 2008) to assess variable importance in the random forest model. Next, we compared model performance for the global model and models with subsets of variables based on changes in the kappa indicator and selected a final model using the kappa indicator. Finally, we evaluated model performance at different prediction thresholds ranging from 0.5 to 0.95 and identified an optimal model using a combination of three model performance indicators: kappa, balanced accuracy, and area under the curve. All models were built using a subset of the clusters, with 80% of the data retained (the training dataset) and evaluated using withheld data (the test dataset). Additional details for the kill prediction model and model performance metrics are available in Appendix 1.

At San Guillermo, large prey consisted of vicuñas and guanacos, while guanacos and lesser rheas (*Rhea pennata*) were considered large prey at the other two sites. Clusters that contained other prey species were excluded from the kill prediction model. We limited our analysis to large prey predation sites (henceforth referred to as predation sites) due to previous work suggesting that pumas do not show evidence of differential habitat selection while hunting primary versus alternate prey species (Cristescu 2019). Additionally, we excluded all investigated clusters from the penguin colony and a 500m buffer around the colony due to extremely low probability of pumas predating primary prey in this region.

Measuring degree of clusteredness and landscape heterogeneity: To account for potential seasonal variation in patterns of space use, we calculated the kernel density home ranges of individuals puma over six-month intervals using the *adehabitat* package in R (Calenge 2006), with the period from December to May identified as 'summer' and the period from June to November identified as 'winter' based on typical precipitation patterns in the region. Next, we calculated the Lloyd's index of patchiness (Lloyd 1967) for (i) all locations used by each individual puma and (ii) predation sites identified by the kill prediction model for each six-month period for which we had location data for the animal. Indices of patchiness were estimated using quadrats measuring 500 square meters. This quadrat size was chosen because it is likely be large enough to include (a) the actual location where the predation event happened given that pumas have been reported to move prey carcasses up to a distance of 80 m (Murphy and Ruth 2010) and (b) other predation or general-use sites in the vicinity. The Lloyd's index of patchiness offers a numerical measure of the degree of aggregation and dispersion in a landscape and is robust to the value of the mean crowding parameter (Lloyd 1967; Wade et al. 2018), allowing us to compare the degree of clusteredness of all used locations and predation sites. Figure 1 shows heatmaps of puma predation sites within home ranges for different values of the Lloyd's index of patchiness, illustrating the differences in space use captured by this metric. To understand landscape heterogeneity, we used four parameters that captured spatial variation: variation in NDVI, variation in slope, variation in elevation and the mean terrain ruggedness index, in line with previous work that analyzed the role of landscape features in puma habitat selection at one of our study sites (Smith et al. 2019a). To measure variation in NDVI, slope and elevation, we

calculated the contagion index value (Li and Reynolds 1993) for the three parameters for the area within the boundaries of each six-month home range. The NDVI and elevation rasters for the contagion index calculations were obtained with Google Earth Engine (Gorelick et al. 2017), using Landsat-8 imagery courtesy of the U.S. Geological Survey for NDVI and the NASA SRTM Digital Elevation dataset (Farr et al. 2007) at 30-meter spatial resolutions. The slope raster was derived from the elevation raster using the *terrain* function in the *raster* package in R (Hijmans & van Etten 2012).

Analysis: We used a Mann-Whitney U test to compare the Lloyd's index of patchiness of predation sites and all-use locations of each puma in each six-month period (prediction 1). To understand how landscape heterogeneity impacts the spatial distribution of puma space use, we built linear mixed models with a combination of variables including the contagion index values for NDVI, elevation and slope, the mean terrain ruggedness index and mean NDVI values as fixed predictor variables. The response variables were the Lloyd's index of patchiness for (a) all used locations (prediction 2a) and (b) predation sites (prediction 2b) for each six-monthly home range for each puma, and (c) the mean daily distance moved during each six-month period as the response variable (prediction 3). We first analyzed data for each site separately to understand site-specific factors that affected puma space use. Subsequently, we combined data across sites to perform an overall analysis to understand broader trends in puma behavior. At the site level, puma ID was used as a random intercept to account for spatial autocorrelation and the repeated measures design of the study. Site was used as a random intercept in the overall models based on the pooled dataset. In case of singular fit issues in the mixed model, we refit the model as a linear model without the random intercept, and differences among individuals or sites were assumed not to explain additional variation in the data. The fixed predictor variables were centered and scaled, and the response variable was log-transformed when highly skewed. All linear mixed models were built using the *lme4* package in R (Bates et al. 2015) and were estimated using restricted maximum likelihood (REML). A detailed summary of all final models, including explanatory power (R^2), is presented in Appendix 2. Finally, we assessed the differences between mean daily distances moved across the three sites using a one-way ANOVA and post-hoc Tukey's HSD test. Clusteredness of all used locations and clusteredness of predation sites across the three study areas were assessed using a Kruskal-Wallis test, followed by a post-hoc pairwise Wilcoxon Rank Sum test with a Benjamin-Hochberg adjustment to assess differences between each pair of study sites.

Results

Puma location data and kill prediction models: Over the period of the study, we obtained location data from 9 individual pumas in San Guillermo, 21 individuals in Patagonia Park and 13 individuals in Monte Leon, with a total of 57,857, 108,027 and 56,617 location points across the three parks, respectively. 2079, 3376 and 2378 clusters were investigated in San Guillermo, Patagonia Park, and Monte Leon, respectively, across the study period, with evidence of a kill found at 411, 952 and 373 of these clusters. The random forest kill prediction models predicted 1093, 1834 and 412 primary prey kills in San Guillermo, Patagonia Park, and Monte Leon respectively across the study period. The number of primary kills in Monte Leon was substantially lower than the other sites due to the strong marine subsidy provided by the penguin colony in the park (Serota et al. 2023). The kill prediction model performance metrics are available in Appendix 1.
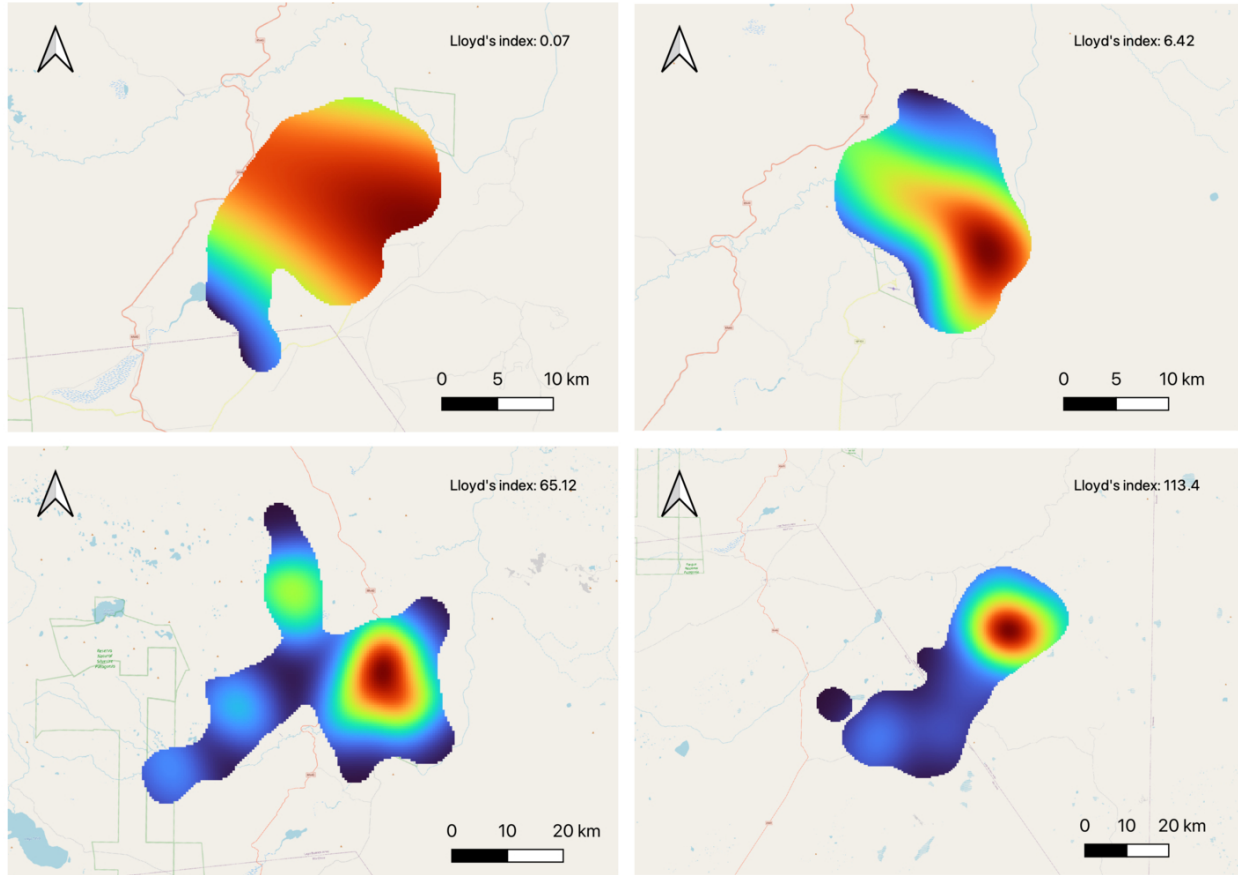
Figure 1: Heatmaps of puma predation sites within home ranges for different values of the Lloyd's index of patchiness, illustrating the differences in space use captured by this metric

Clustering of predation sites and all locations used by pumas: We found evidence to support our hypothesis that pumas use limited areas within their home range for hunting. The Lloyd's index of patchiness for predation sites, using combined data across sites, was 29.81, significantly higher than the value of 18.59 for all used locations (p<0.001). Similar results were obtained at the site level, with values of 26.29 and 13.6 for Patagonia Park (p<0.001), 42.23 and 34.79 for San Guillermo (p=0.001), and 23.26 and 10.87 for Monte Leon (p=0.017). In case of Monte Leon, this result changed to a non-significant difference if all puma locations and clusters in the penguin colony were removed from the analysis. However, these locations were retained in the analysis due to the likely biases introduced by such omission in the estimation of home ranges and home range use. Puma predation sites were thus more clustered than all-use locations. We also found significant inter-site differences in the levels of clusteredness for all-use locations (p<0.001), with pairwise tests revealing significant differences between Patagonia Park and San Guillermo (p<0.001, adjusted using the Benjamin-Hochberg adjustment) and Monte Leon and San Guillermo (p<0.001), but not between Patagonia Park and Monte Leon. Similarly, levels of clusteredness of predation sites were significantly different across sites (p=0.037), with significant differences between Patagonia Park and San Guillermo (p=0.04) and Monte Leon and San Guillermo (p=0.04), but not between Patagonia Park and Monte Leon. Levels of

clusteredness for both all used locations and predation sites were thus significantly higher in San Guillermo than in Patagonia Park and Monte Leon.

Landscape heterogeneity and its impact on space use: Our hypothesis that landscape heterogeneity and structure affects puma space use was partially supported, with different landscape parameters affecting clusteredness across sites. In Patagonia Park, increased variability in slope (p=0.001) reduced the levels of clusteredness of all puma-use locations, whereas increased NDVI (p=0.005) decreased clusteredness of predation sites. In San Guillermo, decreasing variation in NDVI (p=0.02) and increasing mean terrain ruggedness index (p=0.004) increased the levels of clusteredness of all puma-use locations and the clusteredness of predation sites (p=0.002, p=0.017). In Monte Leon, none of the variables examined affected the clusteredness of all puma-use locations or predation sites. Using combined data across sites, increase in variability in slope decreased clusteredness of all-use locations (p=0.008), whereas increase in variability in NDVI decreased clusteredness of predation sites (p=0.034), but an increase in mean NDVI had the opposite effect (p=0.008). While most of the site-level models had moderate explanatory power, the explanatory power of the combined models was low.

Daily movement rates: We found support for our hypothesis that landscape heterogeneity affects puma daily movement rates. In Patagonia Park, increasing variation in slope decreased daily movement rates (p=0.046), and increasing variation in slope (p=0.012) and increasing variation in NDVI (p=0.03) decreased daily movement rates in San Guillermo. In Monte Leon, increased variability in elevation (p=0.008) decreased daily movement rates. At the overall level, using combined data across sites, increased variability in slope (p<0.001) decreased daily movement rates. Details of the site-level and combined models for all locations, predation sites and daily movement rates are listed in Appendix 2 along with significant variables and explanatory power values. Pumas moved an average of 7.79 (+- 1.86) km/day (n=64) in Patagonia Park, similar to Monte Leon, where pumas moved 7.5 (+- 2.31) km/day (n=32), comparable to the daily distances reported from a study in Patagonian Chile (Elbroch and Wittmer 2012). The mean daily distance moved in San Guillermo was 4.25 (+- 1.03) km/day (n=35). A one-way ANOVA revealed significant differences in mean daily movement rates across sites (F=46.78, p<0.001), and a Tukey's post-hoc HSD test revealed significant differences between Patagonia Park and San Guillermo (p<0.001) and between Monte Leon and San Guillermo (p<0.001), but not between Patagonia Park and Monte Leon.

Discussion

We studied the role of landscape structure and heterogeneity on space use by puma at three sites in southern South America. Our analyses revealed that predation sites were more clustered compared to all locations used within the home range, suggesting that hunting activity is limited to a subset of an individual's home range, consistent with the behavior of an ambush hunter. Variation in landscape characteristics appeared to affect space use by pumas across our study sites, with variation in NDVI, variation in slope, mean productivity and terrain ruggedness being important factors affecting space use by these animals. The importance of different landscape variables, however, varied among sites; the generally low explanatory power of our models underscores the expectation that the impact of landscape complexity and variability on space use is highly contextual, suggesting that although puma are typically characterized as ambush hunters, these animals are versatile predators that adopt flexible predation strategies.

Pumas are generally considered ambush hunters (Murphy et al. 1998; Ruth et al. 2019), but this understanding has not been systematically tested. As opposed to coursing predators like wolves, pumas are expected to use limited areas within the landscape, especially while hunting. We found evidence to support this assertion and also found that puma predation sites were more clustered compared to all used locations within the home range. Previous research has produced variable outcomes, with at least one study indicating that behavioral state had little influence on resource selection (Blake and Gese 2016), but another reporting that pumas selected habitat differently while hunting primary prey as opposed to alternate prey (Cristescu 2019). Our within-site analyses revealed similar trends at each of our three study sites. Given that daily distances moved by pumas in San Guillermo were about 45% less than those in both Patagonia Park and Monte Leon, and given that clusteredness for both all-used locations and predation sites were significantly higher in San Guillermo compared to the other two sites examined, we contend that space use by puma in the high Andes differs from that in Patagonian steppe. Vicuñas tend to be sedentary and to utilize limited areas within San Guillermo (Karandikar et al. 2023) and it seems logical that pumas at this site would limit their overall movement to areas that maximize prey encounter and prey capture probabilities (Smith et al. 2020), leading to the differences in space use in San Guillermo versus our other study sites. This result in San Guillermo is also in line with the prey-abundance and prey-catchability hypotheses (Smith et al. 2020).

Landscape heterogeneity and structure affected the spatial distribution of all used locations within puma home ranges, with variation in slope being the most important predictor at an overall level. Decreasing variation in slope in the home range increased the degree of clusteredness of all used locations. Landscapes with large, contiguous patches of homogeneous habitat (lower quality hunting areas) may constrain pumas to use patches with high variability within the home range. The specific factors affecting space use and movement, however, varied across locations. Similar results were obtained for the spatial distribution of predation sites, with variation in NDVI being the most important variable at all sites, with decreasing variation in NDVI associated with increasing degree of clusteredness of all used locations. Landscape heterogeneity, however, affected the levels of clusteredness of predation sites to a lesser extent than all used locations, with limited explanatory power in the site-specific and combined models. We also found support for the hypothesis that predation sites would be more clustered in less productive landscapes (Monk and Schmitz 2021); increasing mean productivity significantly decreased levels of clusteredness of predation sites in Patagonia Park and at an overall level. However, we acknowledge that other factors, including prey availability and behavior, may also play substantial roles in determining how puma kill sites are clustered within the home range.

Puma daily movement rates were significantly affected by landscape heterogeneity and structure across sites, although the specific habitat variables of importance varied across sites, as was observed for clusteredness of locations used by pumas. In general, variation in slope was the best predictor of daily movement rates, with increasing variability in slope decreasing daily movement rates. Pumas in landscapes with gentle and consistent slopes tended to be more sit-and-wait predators that restricted movement to the limited patches of heterogeneity within their home ranges. Consistent with this, pumas in San Guillermo, the site with the greatest variation in slope, moved shorter distances than pumas at the other two sites, with daily movement rates at San Guillermo being more than 20% lower than average rates reported for this species

(Gonzalez-Borrajo et al. 2017). The presumably lower energetic requirements associated with reduced movement rates and the fact that sit-and-wait predators are likely to have lower kill rates than more active predators (Miller et al. 2014) are reflected in the lower effective puma kill rates in San Guillermo compared to Patagonia Park. Puma kill rates in Monte Leon were substantially lower, likely due to the considerable subsidy offered by the penguin colony in Monte Leon (Serota et al. 2023).

Highly adaptable and flexible carnivores like the puma may display considerable plasticity in how they use space within their home range and how they hunt. Pumas in San Guillermo appeared to conform more closely to the classical definition of sit-and-wait or ambush hunters than pumas in the Patagonian steppe that use the landscape more broadly, although this may also be a function of the greater availability of habitat in the sites in the Patagonian steppe that aids stalking or ambushing. Plasticity in hunting behavior has been previously reported in other taxa, including birds, lizards (McLaughlin 1989), spiders (Schmitz 2005), insects (Michel and Adams 2009) and marine and freshwater organisms (Savino and Stein 1982; James and Heck 1994; Hirvonen 1999; Manderson et al. 2000; Laurel and Brown 2006). For example, the wolf spider (*Rabidosa rabida*) is typically a sit-and-pursue strategy hunter but adopts an active hunting strategy when prey abundance drops (Schmitz 2005). Previous research also suggests that the way predators hunt and use space during hunting can change with environmental conditions, including temperature (Barton and Schmitz 2009) and differences in the structural complexity of the landscape (Michel and Adams 2009), although there has been limited research on the effects of variation in landscape complexity on hunting behavior by large, terrestrial predators (Pressier et al. 2007).

Pumas displayed considerable flexibility in behavior and space use across sites, while displaying broadly similar patterns. Deceased heterogeneity likely reduces the number of locations that an ambush hunter like the puma can use, potentially resulting in more limited space use and movement within individual home ranges. This tendency was most evident at San Guillermo (our least heterogeneous site), with pumas at the more heterogeneous Patagonia Park and Monte Leon sites behaving more like coursing predators. While such plasticity in hunting behavior has been reported previously for other taxonomic groups (McLaughlin 1989; Schmitz 2005; Barton and Schmitz 2009), such plasticity in hunting behavior and predation strategies has not been reported in large predator species like the puma. This adaptability may play a critical role in the ability of pumas to thrive in the incredible diversity of habitats and environments used by the species across the Americas. Given the increasing availability of GPS collars with built-in accelerometers, future research should investigate the linkages between these behavioral differences and associated energetic and fitness implications.

Conclusions & Conservation Implications

The ability of pumas to adapt their patterns of space use to changing environmental conditions has important ecological and management implications. Increased clusteredness of predation or general use sites in the landscape can initiate a positive feedback loop that further increases landscape heterogeneity (Monk and Schmitz 2021). For example, if pumas have a spatial anchor (movement within and use of a small area) in a system where prey movement is not similarly restricted, prey 'win' the space race (Sih 2005). This outcome that can dramatically change the

ecosystem in working landscapes such as in the Patagonian steppe, where pumas are often actively persecuted and killed by ranchers and are thus forced to constrain movement to the most rugged parts of the landscape where the chances of detection by ranchers is minimal (pers. obs). From a management perspective, in landscapes where pumas share space with people, identifying areas that are preferentially used by pumas and then avoiding human and livestock activity in those areas can reduce conflict and promote coexistence.

References

Allen, B. L., Allen, L. R., Andrén, H., Ballard, G., Boitani, L., Engeman, R. M., ... & Parker, D. M. (2017). Can we save large carnivores without losing large carnivore science?. *Food Webs*, *12*, 64-75.

Barros, V. R., Scian B. V., & Mattio H. F. (1979). Campos de precipitaciones de la provincia del Chubut (Periodo 1931-1960).

Barton, K. (2009). MuMIn: multi-model inference. http://r-forge. r-project. org/projects/mumin/.

Barton, B. T., & Schmitz, O. J. (2009). Experimental warming transforms multiple predator effects in a grassland food web. *Ecology Letters*, 12(12), 1317-1325.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1-48.

Blake, L. W., & Gese, E. M. (2016). Resource selection by cougars: influence of behavioral state and season. *The Journal of Wildlife Management*, *80*(7), 1205-1217.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral ecology and sociobiology*, 65(1), 23-35.

Calenge, C. (2006). The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological modelling*, 197(3-4), 516-519.

Candino, M., Donadio, E., & Pauli, J. N. (2022). Phenological drivers of ungulate migration in South America: characterizing the movement and seasonal habitat use of guanacos. *Movement Ecology*, *10*(1), 1-14.

Coen, L. D., Heck Jr, K. L., & Abele, L. G. (1981). Experiments on competition and predation among shrimps of seagrass meadows. *Ecology*, *62*(6), 1484-1493.

Cristescu, B., Bose, S., Elbroch, L. M., Allen, M. L., & Wittmer, H. U. (2019). Habitat selection when killing primary versus alternative prey species supports prey specialization in an apex predator. *Journal of Zoology*, 309(4), 259-268.

Donadio, E., Buskirk, S. W., & Novaro, A. J. (2012). Juvenile and adult mortality patterns in a vicuña (Vicugna vicugna) population. *Journal of Mammalogy*, 93(6), 1536-1544.

Donadio, E., & Buskirk, S. W. (2016). Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. *Journal of Mammalogy*, *97*(3), 966-977.

Elbroch, L. M., & Wittmer, H. U. (2013). The effects of puma prey selection and specialization on less abundant prey in Patagonia. *Journal of Mammalogy*, 94(2), 259-268.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J. Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., et al. (2011). Trophic downgrading of planet Earth. *Science*, *333*(6040), 301-306.

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D. & Alsdorf, D. (2007). The shuttle radar topography mission. *Reviews of geophysics*, 45(2).

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of fear: spatial patterns of risk perception and response. *Trends in ecology & evolution*, *34*(4), 355-368.

Gonzalez-Borrajo, N., López-Bao, J. V., & Palomares, F. (2017). Spatial ecology of jaguars, pumas, and ocelots: a review of the state of knowledge. *Mammal review*, 47(1), 62-75.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote sensing of Environment*, 202, 18-27.

Hijmans, R. J., & van Etten, J. (2012). raster: Geographic analysis and modeling with raster data. R package version 2.0-12.

Hirvonen, H. J., & Ranta, E. J. (1999). The game theory approach to size variation, phase 2. In *Size-based tools for managing freshwater fish communities. 2nd Annual Report*, EC Contract No. FAIR CT 96-1957. Norwegian University of Science and Technology.

Holtgrieve, G. W., Schindler, D. E., & Jewett, P. K. (2009). Large predators and biogeochemical hotspots: brown bear (Ursus arctos) predation on salmon alters nitrogen cycling in riparian soils. *Ecological Research*, 24(5), 1125-1135.

James, P. L., & Heck Jr, K. L. (1994). The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *Journal of experimental marine biology and ecology*, 176(2), 187-200.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, *61*(1), 65-71.

Karandikar, H., Serota, M., Sherman, W., Green, J., Verta, G., Kremen, C. & Middleton A. D. (2022). Dietary patterns of a versatile large carnivore, the puma (*Puma concolor*). *Ecology and Evolution*, 12, e9002.

Karandikar, H., Donadio, E., Smith, J. A., Bidder, O. R., & Middleton, A. D. (2023). Spatial ecology of the Vicuña (Lama vicugna) in a high Andean protected area. *Journal of Mammalogy*, *104*(3), 509-518.

Knopff, K. H., Knopff, A. A., Kortello, A., & Boyce, M. S. (2010). Cougar kill rate and prey composition in a multiprey system. *The Journal of Wildlife Management*, 74(7), 1435-1447.

Kuhn, M. (2008). Building predictive models in R using the caret package. *Journal of statistical software*, 28, 1-26.

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*, *79*(8), 1401-1409.

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal*, 3(1).

Laurel, B. J., & Brown, J. A. (2006). Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod Gadus morhua. *Journal of Experimental Marine Biology and Ecology*, 329(1), 34-46.

Li, H., & Reynolds, J. F. (1993). A new contagion index to quantify spatial patterns of landscapes. *Landscape ecology*, 8(3), 155-162.

Lloyd, M. 1967. Mean crowding. *Journal of Animal Ecology*, 36, 1-30.

Manderson, J. P., Phelan, B. A., Stoner, A. W., & Hilbert, J. (2000). Predator–prey relations between age-1+ summer flounder (Paralichthys dentatus, Linnaeus) and age-0 winter flounder (Pseudopleuronectes americanus, Walbaum): predator diets, prey selection, and effects of sediments and macrophytes. *Journal of Experimental Marine Biology and Ecology*, 251(1), 17-39.

McLaughlin, R. L. (1989). Search modes of birds and lizards: evidence for alternative movement patterns. *The American Naturalist*, *133*(5), 654-670.

Michel, M. J., & Adams, M. M. (2009). Differential effects of structural complexity on predator foraging behavior. *Behavioral Ecology*, *20*(2), 313-317.

Miller, J. R., Ament, J. M., & Schmitz, O. J. (2014). Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of animal ecology*, *83*(1), 214-222.

Monk, J. D., & Schmitz, O. J. (2022). Landscapes shaped from the top down: predicting cascading predator effects on spatial biogeochemistry. *Oikos*, 2022(5), e08554.

Murphy, K. M. (1998). *The ecology of the cougar (Puma concolor) in the northern Yellowstone ecosystem: interactions with prey, bears, and humans*. University of Idaho.

Murphy, K., Ruth, T. K., Hornocker, M., & Negri, S. (2009). Diet and prey selection of a perfect predator. *Cougar: ecology and conservation*. University of Chicago Press, Chicago, Illinois, USA, 118-137.

Pauli, J. N., Donadio, E., & Lambertucci, S. A. (2018). The corrupted carnivore. *Ecology*, *99*(9), 2122-2124.

Perrig, P. L., Donadio, E., Middleton, A. D., & Pauli, J. N. (2017). Puma predation subsidizes an obligate scavenger in the high Andes. *Journal of Applied Ecology*, 54(3), 846-853.

Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology*, *88*(11), 2744-2751.

Puig, S., & Videla, F. (2007). Distribución, densidades y estado de conservación de los camélidos. *Diversidad Biológica y Cultural de los Altos Andes Centrales de Argentina*, 198.

Risch, A. C., Frossard, A., Schütz, M., Frey, B., Morris, A. W., & Bump, J. K. (2020). Effects of elk and bison carcasses on soil microbial communities and ecosystem functions in Yellowstone, USA. *Functional Ecology*, 34(9), 1933-1944.

Ruth, T. K., & Murphy, K. (2009). Cougar-prey relationships. *Cougar: Ecology and Conservation. The Univ. of Chicago Press, Chicago*, 138-155.

Ruth, T. K., Buotte, P. C., & Hornocker, M. G. (2019). *Yellowstone cougars: ecology before and during wolf restoration*. University Press of Colorado.

Salvioli, G. (2007). Caracterización hidrometeorológica. *Diversidad biológica y cultural de los Altos Andes Centrales de la Argentina: línea de base de la reserva de la biosfera San Guillermo*, 63-87.

Savino, J. F., & Stein, R. A. (1982). Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society*, 111(3), 255-266.

Schmitz, O. J. (2005). Behavior of Predators and Prey and Links with Population-Level Processes. In *Ecology of predator-prey interactions*, 256-278, Oxford University Press, Oxford, UK.

Schmitz, O. J. (2007). Predator diversity and trophic interactions. *Ecology*, *88*(10), 2415-2426.

Schmitz, O. J. (2008). Effects of predator hunting mode on grassland ecosystem function. *Science*, *319*(5865), 952-954.

Serota, M. W., Alarcón, P. A., Donadio, E., & Middleton, A. D. (2023). Puma predation on Magellanic penguins: An unexpected terrestrial-marine linkage in Patagonia. *Food Webs*, e00290.

Sih, A. (2005). Predator-prey space use as an emergent outcome of a behavioral response race. *Ecology of predator-prey interactions*, 256, 78.

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., & Middleton, A. D. (2019a). Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places. *Oecologia*, *189*(4), 883-890.

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., Bidder, O. R., & Middleton, A. D. (2019b). Habitat complexity mediates the predator–prey space race. *Ecology*, *100*(7), e02724.

Smith, J. A., Donadio, E., Bidder, O. R., Pauli, J. N., Sheriff, M. J., Perrig, P. L., & Middleton, A. D. (2020). Where and when to hunt? Decomposing predation success of an ambush carnivore. *Ecology*, 101(12), e03172.

Wade, M. J., Fitzpatrick, C. L., & Lively, C. M. (2018). 50-year anniversary of Lloyd's "mean crowding": Ideas on patchy distributions. *Journal of Animal Ecology*, 87(5), 1221-1226.

Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal Society open science*, *4*(7), 170052.

Appendices

Appendix 1: Kill prediction model

(a) Model details

Site	Method used	Variables used in the prediction model
Patagonia Park	Random Forest	Number of cluster locations, altitude, hour of first point in the cluster, fidelity to the cluster, maximum foray distance from the cluster centroid, cluster radius, NDVI, terrain ruggedness, month of cluster formation and Animal ID (random factor)
San Guillermo	Random Forest	Number of cluster locations, altitude, hour of first point in the cluster, fidelity to the cluster, maximum foray distance from the cluster centroid, cluster radius, NDVI, terrain ruggedness, month of cluster formation and Animal ID (random factor)
Monte Leon	Random Forest	Number of cluster locations, altitude, fidelity to the cluster, maximum foray distance from the cluster centroid, cluster radius, month of cluster formation and Animal ID (random factor)

(b) Model performance metrics

Site	Threshold to classify kill	Mean Accuracy	Mean Kappa	Mean Balanced Accuracy	Mean Sensitivity	Mean Specificity	Area under the curve
Patagonia Park	0.68	0.89	0.63	0.83	0.73	0.92	0.83
San Guillermo	0.63	0.9	0.73	0.88	0.84	0.91	0.88
Monte Leon	0.62	0.94	0.63	0.82	0.67	0.97	0.82

Appendix 2: Best site-level and combined models for all locations, predation sites and daily movement rates

All-use locations

Site	Significant variables	Explanatory power (Marginal, Conditional)

Patagonia Park	Variation in slope	0.27, 0.66
San Guillermo	Variation in NDVI Mean terrain ruggedness	0.28, 0.57
Monte Leon	None	0.26, 0.43
Combined	Variation in slope	0.12, 0.4

Predation sites

Site	Significant variables	Explanatory power (Marginal, Conditional)
Patagonia Park	Mean NDVI	0.15, 0.41
San Guillermo	Variation in NDVI Mean terrain ruggedness	0.3, 0.53
Monte Leon	None	0.06 (no random effect)
Combined	Variation in NDVI Mean NDVI	0.1 (no random effect)

Daily movement rates

Site	Significant variables	Explanatory power (Marginal, Conditional)
Patagonia Park	Variation in slope	0.23, 0.68
San Guillermo	Variation in NDVI Variation in slope	0.52 (no random effect)
Monte Leon	Variation in elevation	0.23, 0.67
Combined	Variation in slope	0.22, 0.67

In the previous chapter, I demonstrated how animals can demonstrate considerable flexibility in space use and movement due to environmental factors that support or impede specific behavioral traits. In the next chapter, I assess animal movement at the species' range level, with an objective of understanding how habitats, and thus environmental and anthropogenic factors, can facilitate or inhibit longer-distance movements. This understanding can help inform range-level species' strategies.

Chapter 3: Identifying priority corridors for Jaguar conservation in the Americas

I acknowledge the significant inputs from Robin Naidoo for this chapter.

Abstract

Despite the on-going recovery of large carnivore populations in many parts of the world, habitat loss and reduced connectivity threaten the long-term persistence of many of these species across their ranges. Understanding connectivity and dispersal routes between carnivore metapopulations can significantly add to existing carnivore conservation strategies, and telemetry data from GPS collars have the potential to strengthen these analyses. Using location data from over one hundred individual jaguars (*Panthera onca*), we assessed the connectivity between key populations of this species across its range in Mexico, Central America, and South America. Specifically, we identified critical corridor areas to promote dispersal and movement among Jaguar Conservation Units (JCUs), regions supporting viable populations of jaguars. Conservation efforts that include land-use change scenarios that may impede jaguar movement through these corridor areas are essential for maintaining healthy and stable populations of the largest felid species in the Americas.

Introduction

Despite the myriad threats that several large carnivore species face, many of these iconic species, including tigers (*Panthera tigris*) (Jhala et al. 2019), pumas (*Puma concolor*) (Walker et al. 2010), and wolves (*Canis lupus*) (Burke 2020) have seen strong recoveries in terms of numbers and recolonization of historic parts of their range over the last few decades. Although these are important conservation wins, continued habitat loss, especially outside protected areas (PAs), and impediments to connectivity between carnivore populations, remain significant challenges that threaten the long-term persistence of these species (Crooks et al. 2011). While protected areas may continue to play an integral role in large carnivore conservation efforts, the long-range dispersal events and use of human-dominated landscapes often observed in these species (Athreya et al. 2013) means that landscape-level planning and strategies that identify and prioritize key areas outside PAs are important for large carnivore conservation at the range level.

Corridors are a vital tool in landscape-level conservation planning, playing a critical role in connecting habitat patches that can aid dispersal within and between metapopulations (Crooks and Sanjayan 2006; Gilbert-Norton et al. 2010). In a world with increasingly fragmented natural landscapes, corridors connect isolated populations and islands of habitat, increasing gene flow and genetic diversity and strengthening the ability of species to recolonize suitable habitats after local extinction events. Corridors have been shown to be effective and improve connectivity across taxonomic groups, including terrestrial vertebrates except birds (Gilbert-Norton et al. 2010), and are considered important even when large protected areas exist (Newmark 1987). Although possibly less important for wide-ranging species that inhabit a diverse range of habitats, corridors may also be an important bulwark against the impacts of climate change. Wildlife conservation planning that emphasizes corridor conservation can also contribute towards the development of more holistic, all-round strategies that achieve conservation while

considering humans and working lands as an integral part of landscapes and strengthening co-existence.

The jaguar (*Panthera onca*), the bigger of the two large felid species in the Americas, exemplifies many of the conservation challenges faced by large carnivores (Quigley et al. 2017). Unlike pumas, jaguars are restricted to the tropical and subtropical parts of the continent from Northern Mexico to Northern Argentina (Medellin et al. 2016), regions that continue to face large-scale land-use change and habitat loss and fragmentation. Jaguar diets also consist of considerably fewer prey species than pumas (Hayward et al. 2016; Karandikar et al. 2022), likely limiting the former species' ability to adapt to intensive human-use landscapes. Similar to the puma, however, jaguars are persecuted in most parts of their range due to conflict with humans, primarily in the form of livestock depredation (Zimmermann et al. 2021). A combination of these factors and other threats have contributed to jaguars being extirpated from over half of their original range over the last century (Sanderson et al. 2002; De La Torre et al. 2018). Although the jaguar is currently classified as 'Near threatened' (Quigley et al. 2017), a recent analysis suggests that this species likely faces a higher level of threats across its range, especially for populations outside the Amazonian region (De La Torre et al. 2018). In recognition of these threats and the importance of adopting a landscape-level approach, a range-wide research and conservation plan for the species was developed in the early 2000s, with support from a large number of jaguar researchers and organizations working on jaguar conservation (Sanderson et al. 2002). This exercise identified critical Jaguar Conservation Units (JCUs), geographic areas that harbored healthy and viable jaguar populations. The JCU network continues to be updated and modified to enable optimal conservation strategies and on-ground actions (WWF 2020).

Jaguars have been known to undertake long-range dispersal movements that can span over a hundred kilometers (Wildlands Network 2022). While studies from a few decades ago suggested little genetic differentiation between jaguar populations (Eizirik et al. 2001; Johnson et al. 2002; Ruiz-Garcia et al. 2006), recent genetic analyses highlight the connectivity challenges for jaguars. Recent studies suggest four genetically differentiated regions across the species' range and evidence of genetic decline in the last two-three decades (Roques et al. 2015). An analysis focused on mesoamerica revealed moderate levels of genetic variation (Wultsch et al. 2016). The situation may be more dire in the Atlantic Forest region in Brazil, with marked genetic differentiation among and recent allelic loss in populations from this region (Haag et al. 2010). These changes point towards increasingly isolated jaguar populations, further highlighting the importance of corridors as a vital component of successful long-term strategies for jaguar conservation.

Since the development of the range-wide initiative, several studies have assessed and identified potential corridor areas that connect JCUs across or in parts of the jaguar range (Rabinowitz and Zeller 2010; Zeller et al. 2013; Diniz et al. 2017; Thompson and Velilla 2017). Most of these studies used structural connectivity (i.e., the environmental, terrain and other characteristics that may facilitate or prevent movement across habitat patches), assessed through expert inputs, as a surrogate for functional connectivity (i.e., identified areas that may facilitate or prevent movement, derived from a combination of recorded animal movements and habitat variables) to predict jaguar movement between JCUs. The increasing availability of telemetry data from GPS collars offers an opportunity to develop an understanding of realized jaguar movement and

dispersal that can validate expert-opinion based assessments. In the case of large felid species in particular, second-order resource selection (i.e., selection in a home range) can be effectively used as a surrogate to assess functional connectivity due to the fact that habitat selection by dispersing animals is similar to that by other adult individuals (Fattebert et al. 2015).

In this analysis, we used jaguar GPS telemetry data to understand and map connectivity across the species' range, with an objective of identifying important corridors that need conservation focus and action over the next few decades. First, we used jaguar location data to model longer-range jaguar movements and used this to obtain a range-wide understanding of jaguar habitat selection during these movements. Next, we used this understanding of jaguar habitat selection to map how jaguars would likely move between specific jaguar habitats within the species' range. Finally, we used these connectivity maps to identify specific corridor areas that likely support jaguar movement and compare these with previously identified corridors (Rabinowitz and Zeller 2010; Zeller et al. 2013).

Methods

Study area: We analyzed jaguar connectivity in a region spanning northern Mexico to the southern end of the species' current range in northern Argentina (Sanderson et al. 2002; Quigley et al. 2017). Between the northern and southern limits of the species' geographic range, we included areas that currently do not hold jaguar populations to enable us to identify all corridor areas that may support jaguar movements, now or in the future.

Data: We used a publicly available GPS telemetry dataset consisting of 134,690 locations of 117 individual jaguars from across the range of the species (Morato et al. 2017). Additional information about the dataset, including demographic data on collared individuals, frequency of GPS location fixes for each individual, study locations and duration of each study are available in the supporting information files for Morato et al. 2017. Based on consultations with several jaguar researchers with significant understanding of jaguar movement and behavior, we identified 13 environmental and 8 anthropogenic variables (Table 1) that were likely to support or inhibit jaguar movement. Datasets were downloaded from Google Earth Engine (GEE) (Gorelick et al. 2017) and other sources (Table 1) and subsequently processed in R, using RStudio, QGIS and ArcGIS Pro. For environmental variables that were likely to have changed significantly over the last few decades, we first used historical data at or approximately around the time when the jaguar was present in the area to build the movement model, while using current data to build the predicted output layer from the step selection function (SSF) model (explained below). The list of identified variables and the variables eventually used in the movement model, along with the specific sources for each dataset, are listed in Table 1.

Modeling jaguar movement: Resource selection functions (RSFs) (Manly et al. 2007) have been used widely in ecology over the last few decades to understand animal resource selection, space use and movement in a wide variety of taxonomic groups. Within this broad category of models, animal movement can be analyzed using different methods that focus either on (1) resource selection at actual point locations used by the animal (point selection functions), (2) at the start and end of 'steps' (two or more consecutive locations) (SSFs), and (3) along a path (comprising several steps, usually constrained by a time window) (path selection functions, PathSFs). Among

these methods, SSFs and PathSFs are generally considered superior to point selection functions (Zeller et al. 2012), with PathSFs often outperforming SSFs (Zeller et al. 2016). Due to data limitations, we modeled jaguar movement with SSF models, despite the reported superior performance of PathSFs. Because our location data are a collated dataset across several independent studies over more than 15 years, location frequencies varied considerably across the studies in the database. Since SSFs use 'steps' comprising sequential locations for individual animals, we subsampled the dataset to one location fix per animal per 24 hours. While this resulted in data loss within individuals (for example, for an animal with a frequency of 1 location/6 hours, we lost the data at hours 6, 12 and 18, and retained points at hours 0 and 24), this ensured that we retained data from a significantly larger number of individual jaguars in the dataset than possible with a higher sampling frequency (individuals with lower location frequencies would be completely eliminated from a high-frequency dataset due to the inability of the step-generation algorithm to generate steps with sequential points). The choice of SSFs over PathSFs was justified due to this low sampling frequency, given the likely considerable differences between the actual path of the animal and the straight-line path used to determine covariate values with low-frequency location fixes. This subsampling also ensured that we retained more longer-range movements and eliminated shorter movements within small areas of the animal's home range. For the same objective of retaining longer-range movements, we additionally only retained steps with a step-length greater than 1000 m in the dataset. We used the *amt* package in R to create 'tracks' for each animal and to perform these sub-selections (Signer et al. 2019).

Candidate Variables	Central America	Amazon	Pantanal	Dataset and source[+]
Environmental variables				
Mean NDVI	✓	✓		Landsat 7; GEE
Mean NPP[#]				MODIS GPP/NPP Project; GEE
Tree cover			✓	Global Forest Cover Change Tree Cover Multi-Year Global; GEE
Land cover (shrub, grass, crop, bare, herbaceous wetlands)	✓*	✓*	✓*	ESA WorldCover; GEE
Annual precipitation			✓	WorldClim version 2.1 climate data; https://worldclim.org
Distance to water	✓	✓	✓	ESA WorldCover; GEE
Density of water	✓	✓	✓	ESA WorldCover; GEE

Elevation			✓	NASA SRTM Digital Elevation; GEE
Slope	✓	✓		NASA SRTM Digital Elevation; GEE
Terrain ruggedness[#]				NASA SRTM Digital Elevation; GEE
Distance to a Protected Area		✓	✓	Protected Planet WDPA dataset; https://protectedplanet.net
Density of Protected Areas[#]				Protected Planet WDPA dataset; https://protectedplanet.net
Anthropogenic variables				
Distance to nearest road		✓	✓	OpenStreetMap; https://openstreetmap.org
Density of roads	✓	✓	✓	OpenStreetMap; https://openstreetmap.org
Distance to nearest built-up area	✓	✓	✓	ESA WorldCover; GEE
Density of built-up area[#]				ESA WorldCover; GEE
Density of night lights		✓	✓	Nasa Black Marble; https://blackmarble.gsfc.nasa.gov
Human population density	✓	✓	✓	Socioeconomic Data and Applications Center, Columbia University; https://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-density-rev11
Distance to navigable water	✓			Venter et al. 2016; https://datadryad.org/stash/dataset/doi:10.5061/dryad.052q5
Barrier effect of road		✓	✓	OpenStreetMap; https://openstreetmap.org

* Not all categories used in each model

+ Several variables were derived from the raw data listed here
 # Some variables were not used in any of the sub-regional models

Table 1: Candidate variables and variables used in the 3 sub-regional models

We divided the jaguar range into three broad parts (subsequently referred to as sub-regions for clarity), and built separate SSF models for each sub-region, with the objective of developing models that incorporate differences in jaguar habitat selection across the range. Each sub-region included overlaps with other regions in order to achieve an understanding of overall connectivity across the range. The first sub-region comprised all of Central America and Mexico, with the northern parts of South America that connect with the isthmus comprising the Darien gap, henceforth referred to as the Central American sub-region. The second sub-region focused on the Amazon, extending northwards into the Darien gap and southwards into the northern parts of the Pantanal, referred to as the Amazon sub-region. The third sub-region included the Pantanal and Atlantic Forest regions, extending to the southern end of the jaguar range, referred to as the Pantanal sub-region. To build the models, we first subsampled the jaguar location dataset for each sub-region. Then, to reduce codependency of model factors, we removed 1 variable from each pair of variables that were related to each other with a correlation coefficient greater than 0.7. Next, we built conditional logistic regression models with (a) the retained variables and (b) transformed values of the retained variables, determined based on the distribution of each variable and the possible biological relevance of the transformed values. Conditional logistic regression (Agresti 2012) offers a more appropriate framework for evaluating the used-available data structure employed in SSFs. To measure the predictive performance of the two models for each sub-region, we used the Continuous Boyce Index (Hirzel et al. 2006), with 100 iterations per sub-region. The list of variables used in the final model for each sub-region is provided in Table 1. The coefficients of the SSF model can be used to generate a predicted habitat raster, which represents a permeability layer that offers a landscape-level map of areas that impede or support movement. We thus used the final sub-regional models to generate a permeability raster layer for each of the three regions, using the *amt* package in R (Signer et al. 2019). Lastly, we converted this layer to a resistance layer by inverting the values.

Assessing connectivity and identifying corridors: Circuit theory and Least Cost Paths are two commonly used methods to model connectivity between animal populations (Rainey 2012; Marrotte and Bowman 2017). The circuit theory approach models connectivity in the landscape in the form of flow of electrical current (McRae 2008; Dickson et al. 2019), with the areas with the highest current flows likely representing the most suitable areas for animal movement. Least Cost Paths calculate the accumulated 'costs' of moving through the landscape (Adriaensen et al. 2003). A resistance layer, in this case the inverse of the predicted habitat raster layer, is used as an input for both methods. An additional input required are the sources and destinations of animal movements; these are termed nodes in the circuit theory approach and start and end points in the Least Cost Paths approach. Although there are key conceptual differences between the two methods, they are complementary in terms of identifying raster cells that support or impede movement, and should identify similar areas in the landscape that support connectivity (Rainey 2009, but also see Marrotte and Bowman 2017). The circuit theory approach offers an advantage in that it inherently factors in the uncertainty associated with paths that are likely to be used, and suggests alternate movement pathways, compared to the least cost path approach that

suggests a single 'best' path (although additional likely paths may be identified with this approach). Since the objective of this analysis was to identify corridors that connect key jaguar habitats, we first employed the circuit theory approach, using the Circuitscape application (McRae et al. 2016). For each of the three sub-regions analyzed, we used the centroids of the JCUs (WWF 2020) as the input nodes for Circuitscape. Next, we compared the corridors identified through Circuitscape using the least cost paths approach, as implemented in the *leastcostpath* package in R (Lewis 2022).

Although this approach was effective in identifying connectivity between JCUs, it ignored some parts of the jaguar range and consequently might not have necessarily offered a complete picture of connectivity across the range. To address this shortcoming and to validate the corridors identified between JCUs, we used Protected Areas (PAs) from the World Database on Protected Areas (UNEP-WCMC and IUCN 2022), that were (a) subsampled for the sub-region, (b) designated as 'national' in their descriptions, (c) not classified as 'Marine' PAs and (d) at least 100 km^2 in size. From this subset, we randomly sampled 10 PAs in the Central American sub-region and 20 PAs each in the Amazon and Pantanal sub-regions and used their centroids as the input nodes for Circuitscape. We repeated the random sampling ten times and averaged the Circuitscape output rasters generated during each iteration to obtain a connectivity map for each sub-region. Corridors were identified from the connectivity maps generated from both approaches, i.e. (a) between JCUs and (b) the averaged raster using sampled PAs.

Results

For all three sub-regions, the SSF model with transformed variables outperformed the model with untransformed variables, based on the values of the Continuous Boyce Index. The average values of the Continuous Boyce Index over 100 iterations for each of the three regions were 0.75, 0.32 and 0.52 for the for the Central American sub-region, the Amazon sub-region and Pantanal sub-region respectively, indicating moderate to high predictive ability for all sub-regions. The permeability layers for the three

Figure 1: Permeability rasters for the three sub-regions

sub-regions, generated with the SSF models, are shown in Figure 1. These layers show jaguar habitat selection while moving through the landscape.

Figure 2 offers a range-level perspective of jaguar connectivity, while figures 3, 4, 5 and 6 consist of sub-regional maps with identified corridor areas derived by using JCUs and PAs. Figure 3a and 3b show corridors in the Central American sub-region extending south to the northern boundary of Panama, using JCUs and sampled PAs as nodes respectively. Figure 3a, 5a and 6a also include the least cost paths identified between JCUs. Although the area in Panama and parts of Colombia connecting South America with the Central American isthmus are a part of the Central American sub-region for this analysis, this area is shown separately in Figure 4 for greater clarity in identifying corridors in this narrow region, with only the Circuitscape output with JCUs as nodes shown, due to the absence of any additional corridors identified using PAs as nodes. Figure 5a and 5b show the connectivity in the Amazon sub-region, while 6a and 6b show connectivity in the Pantanal sub-region.
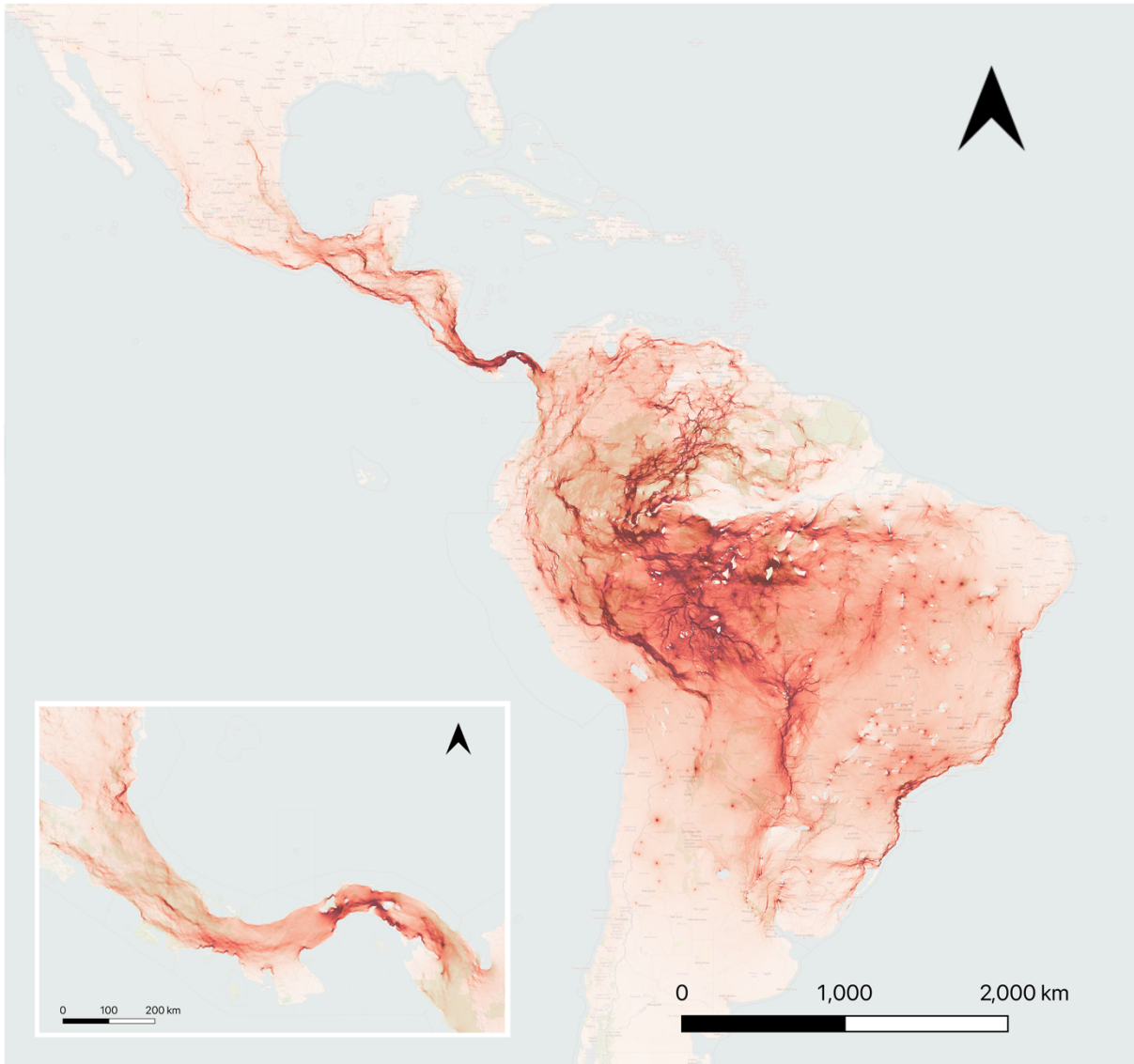
Figure 2: Connectivity and movement pathways across the jaguar range. The inset map shows this in Panama and the isthmus connecting Central America with South America, a region that is saturated in the range-level map

In the Central American sub-region north of Panama, we identified four key sets of corridors (Fig 3a and 3b). The first (marked 1) connects west-central Mexico to the eastern end of Oaxaca state, along the Pacific coast. The second major corridor here (marked 2) runs from the eastern end of Oaxaca to Panama along the Pacific coast, using the narrow strip of land on the south-western edge of Lake Nicaragua. The third important pathway (marked 3) connects the Mayan peninsula to the Panama border more or less along the Atlantic coast with some forays inland, through Guatemala, Honduras, Nicaragua, and Costa Rica. The last important corridor (marked 4 in Figure 3b) connects the isthmus region in eastern Oaxaca with a region just south of Monterrey, running parallel to, but at some distance from, the Atlantic coast. The least cost paths highlight several additional connections between these pathways, including an east-west connection in central Mexico, several connections across the Mayan peninsula and one

connecting the southern end of the Mayan peninsula with the second major corridor (marked 2) that runs along the Pacific coast. In the southern part of the Central American sub-region comprising southern Costa Rica, Panama and the part of Colombia connecting South America to the isthmus, our analysis identified a pathway that largely used the southern side of this region (Figure 4).
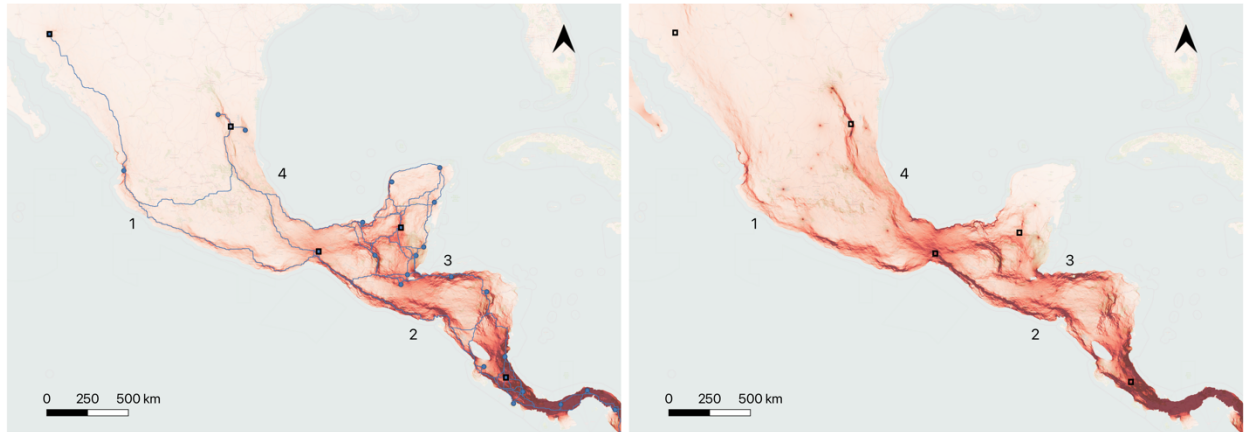

Figure 3: Movement pathways in the Central America sub-region; (a) Movement pathways and least cost paths identified using JCUs (blue dots) and (b) Movement pathways identified using randomly sampled PAs. In both maps, a deeper red color signifies better connectivity routes and the black boxes signify the start and end of corridors. Blue lines in the map on the left show the least cost paths.

The Amazon sub-region largely comprises a network of routes that crisscross across the region. Within this, we identified several long-distance movement routes that connect distinct areas within this large sub-region, shown in Figures 5a and 5b, and marked with numbers on the maps. The first connects areas in the western Amazon in Ecuador, Colombia and Peru with areas to the south, in western Brazil. Another route starts from the same region in the Western Amazon and goes eastwards towards north-western
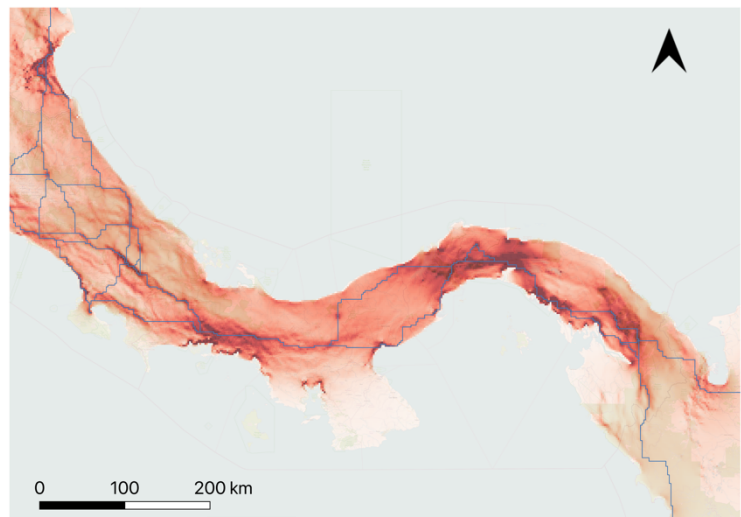

Figure 4: Movement pathways in the southern part of the Central America sub-region

Brazil, before turning north-eastwards to end in the border region between northern Brazil, Venezuela and Guyana. A third route connects the areas in western Brazil with areas along the Amazon river and eventually to route 2. The fourth large route connects the end of route 2 with key JCUs in the northernmost parts of the region, along the boundary between Venezuela and Colombia. Route 5 completes this large loop, connecting the border areas between Venezuela and Colombia with the starting area of the first route. The connectivity map generated with protected areas offer 2 additional long routes: route 6 that flanks the northern banks of the Amazon and route 7 that flanks the southern bank, both in a west-east direction.
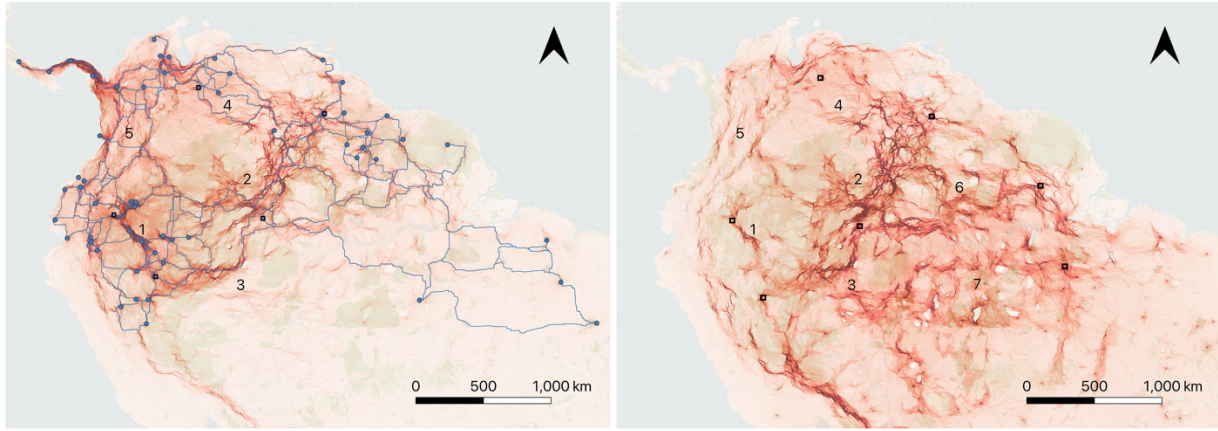
Figure 5: Movement pathways in the Amazon sub-region; (a) Movement pathways and least cost paths identified using JCUs (blue dots) and (b) Movement pathways identified using randomly sampled PAs. In both maps, a deeper red color signifies better connectivity routes, and the black boxes signify the start and end of movement pathways. Blue lines in the map on the left show the least cost paths.

We identified five long-distance connecting routes in the Pantanal sub-region, considered as a critical part of the jaguar range (Sanderson et al. 2002), marked with numbers in Figures 6a and 6b. The first starts in Peru, just across the western end of the border with Brazil and goes in a south-easterly direction till the eastern end of Bolivia. The second comprises two routes that largely run in parallel, starting in northern Bolivia and moving north-eastwards towards the Amazon river. The third starts in the eastern end of Bolivia, at the end of the first route, and extends southwards till just north of Asuncion, the capital of Paraguay, on the floodplains of Rio Paraguay and follows the river. The fourth route starts from the Amazon river near Santarém in Brazil and moves eastwards towards the coast. The last major route in this sub-region is along the Atlantic coast in east to south-eastern Brazil.
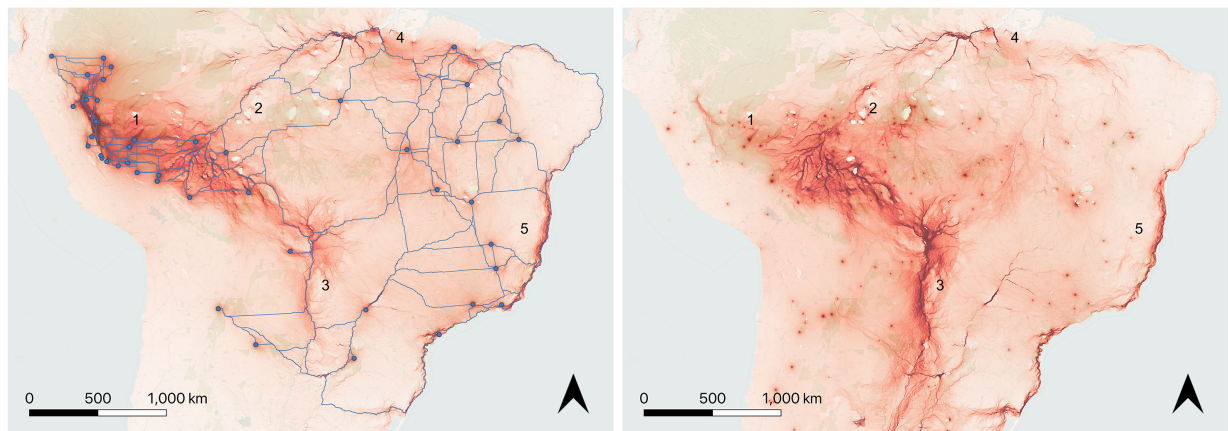

Figure 6: Movement pathways in the Pantanal sub-region; (a) Movement pathways and least cost paths identified using JCUs (blue dots) and (b) Movement pathways identified using randomly sampled PAs. In both maps, a deeper red color signifies better connectivity routes, and the black boxes signify the start and end of movement pathways. Blue lines in the map on the left show the least cost paths.

Discussion

We present the first range-level analysis of connectivity using GPS telemetry data for the jaguar, building on previous work that has assessed the connectivity threats and priorities for the species (Rabinowitz and Zeller 2010; Zeller et al. 2013). Our analysis confirms the importance of previously identified jaguar movement corridors (Figure 2 in Rabinowitz and Zeller 2010; Figure

1 in Zeller et al. 2013), while also identifying new movement routes that animals are likely to use and can inform range-level jaguar conservation strategies.

In Central America, the corridors labelled 1 and 3 closely match the results from previous studies (Rabinowitz and Zeller 2010; Zeller et al. 2013), including one corridor categorized as a corridor of concern; however, the other two large corridors (marked 2 and 4) have not been previously identified as important regions for jaguar connectivity. Corridor 2, however, comprises areas along the pacific coast of Guatemala, El Salvador and Nicaragua; these areas are not currently considered a part of the extant jaguar range (Quigley et al. 2017). Given that the objective of this analysis is to identify potential corridor areas within the geographic boundaries of the jaguar range, we suggest that this corridor be considered as a potential future jaguar recovery area that may also significantly strengthen connectivity and offer an important alternative movement route within this region. Our analysis, however, did not identify the corridor of concern identified in these previous studies (Rabinowitz and Zeller 2010; Zeller et al. 2013), in northern Mexico, suggesting that a critical connectivity pathway between the Monterrey area and the area north of Guadalajara, through north-central Mexico, might no longer support jaguar movement. Lastly, the southern part of this sub-region, primarily consisting of areas in Panama, comprises a part of the jaguar range that is an especially challenging area to study and assess for jaguar movement due to challenges associated with accessing the region, safety issues and the fact that given the nature of the terrain and the habitat, jaguars likely can use several pathways to move through this region while avoiding interactions with people.

Identifying specific, clearly delineated corridors is challenging in the Amazon sub-region due to the large patches of intact habitat in the Amazon and surrounding regions. As expected for this region, several alternative pathways exist for jaguar movement between the several JCUs in this region. Most of the routes identified in this analysis for this region match those from previous studies (Rabinowitz and Zeller 2010; Zeller et al. 2013), with the exception of the network of paths that comprise route 5 in the northwestern part of this sub-region. With several parallel and crisscrossing paths, our analysis suggests that jaguars moving through this region have several alternative routes that may be used. A key difference between our results from the Amazon sub-region and the results from previous work is the limited number of connectivity routes in our analysis across the Amazon river, especially in the areas downstream of Leticia in Colombia. Although jaguars are known to be adept swimmers (Eisenberg et al. 2014; dos Santos Ramalheira et al. 2015), with freshwater reptiles an important part of their diet in Amazonia (Da Silveira et al. 2010), very large, fast-moving water bodies like the Amazon river may still be impediments to jaguar movement. This is also reflected in the results of the analysis done with protected areas, which shows two areas with high connectivity (numbered 6 and 7) that run along the river on the northern and southern side, which were not identified as important movement routes in previous work. Lastly, the regions in eastern Brazil seem to have limited connectivity with the key jaguar areas in the central and western Amazon.

In the Pantanal sub-region, jaguar movement as per the model is closely aligned with rivers. This is in line with previous studies that suggest that jaguars stay in close proximity to large water bodies in the region due to the greater availability of prey in the form of livestock in these parts, especially in the dry season (Gese et al. 2018). The first two routes from our analysis are similar to those identified in previous studies (Rabinowitz and Zeller 2010; Zeller et al. 2013). The third

route, heading north to south along Rio Paraguay appears to replace a mesh of pathways identified in these previous studies, with limited connectivity away from the river. Route 4, running along the Amazon River, also differs from the pathways identified in these previous studies (Rabinowitz and Zeller 2010; Zeller et al. 2013). In this region, along the Amazon River, our models for the two sub-regions (Amazon and Pantanal) suggest different routes: the Amazonian model identifies movement corridors to the north and south of the river, whereas the Pantanal model suggests that jaguars follow the river stream and important tributaries. Finally, the fifth long-distance route identified in our analysis, running along the coastal areas of southeastern Brazil also was not identified in previous studies. This route uses large parts of the Atlantic forests, including the Bahia coastal forests and the Serra do Mar coastal forests. While considerable intact habitat still remains in the Serra do Mar coastal forests (SOS Mata Atlântica 1998), less than 5% of the original habitat remains in the highly threatened Bahia coastal forests (Viana et al. 1997). Most of the JCUs in the Atlantic Forest area have limited connectivity with other parts of the jaguar range and with the strong other routes identified in this analysis, and appear considerably isolated from the other JCUs, in line with previous studies that identify several corridors of concern in this area (Rabinowitz and Zeller 2010; Zeller et al. 2013). We propose the evaluation of this corridor route, along with an evaluation of levels of genetic isolation in the jaguar populations in the Atlantic Forest region on a priority basis. Also, given the limited connectivity in this part of the jaguar range, urgent conservation efforts need to be undertaken to protect this important connectivity route for the species. From a broader perspective, with the Pantanal seeing high levels of deforestation and land-use change (D'Acunha et al. 2021), and a recent study estimating that only 9.3% of jaguar habitats in the Pantanal under protection (Alvarenga et al. 2021), the corridors in these regions gain even more importance.

Our study identifies possible critical corridors that connect JCUs and other known or likely jaguar habitats across the range of the species and offers the first estimates of these routes based on actual jaguar presence and movement data. We acknowledge the several limitations and challenges associated with our approach. One, although our dataset comprised location data from over a hundred individual jaguars, jaguar data availability is limited to pockets within the species' range. Developing sub-regional or range-level connectivity maps from such data inevitably includes an extrapolation of results to distant areas and regions, with likely different habitat conditions and threats to jaguar persistence and movement. Future assessments that incorporate data from camera-trap studies or include additional GPS telemetry datasets in the jaguar range thus have the potential to improve on the results of our study. Two, the considerable variation in fix rates across individuals and studies in the jaguar location dataset represented challenges in modeling the data and required subsampling that caused significant data loss for several individuals. Additional data loss occurred when we filtered movement 'steps' for a minimum distance of 1 km as a proxy for only retaining longer-range movements. Future studies that have access to more regular, finer-scale data can identify movements specifically linked to dispersal using behavioral classification methods such as net-squared displacement (Bunnefeld et al. 2011) and Hidden Markov Movement Models (McClintock et al. 2020). Such fine-scale data may also make the use of PathSFs more appropriate for this analysis (Zeller et al. 2012). Finally, we recognize the fact that many large felids demonstrate high behavioral plasticity and are extremely adaptable animals that can modify behavior based on changing habitat conditions. Pumas, for example, demonstrated significant differences in space use, movement, and predation

patterns across habitats (Karandikar et al. in prep), whereas leopards have been known to persist in highly human-dominated landscapes (Athreya et al. 2013). While modeling areas suitable for jaguar movement offers an estimate of ideal routes, the possibility of jaguars using other sub-optimal regions and pathways cannot be ruled out.

Statistical models are thus only the first step in this process, and we recognize the importance of ground-truthing and other validation methods to confirm and improve upon the results of our analysis. Several tools and methods can achieve this, including but not limited to (i) genetic analysis of populations, (ii) estimating jaguar use of corridors using camera traps and sign surveys, (iii) using local community knowledge of jaguar presence and movement and (iv) long-term collaring studies. Genetic analyses across populations are important in identifying isolated populations and can further help prioritize corridors for conservation. This is particularly relevant given the alarming drop in connectedness between populations reported in recent studies (Haag et al. 2010; Roques et al. 2015; Wultsch et al. 2016), compared to studies conducted about two decades ago (Eizirik et al. 2001; Johnson et al. 2002; Ruiz-Garcia et al. 2006). Conducting jaguar sign surveys, including the use of dogs trained for scat-detection in priority corridors identified through this study can confirm jaguar movement through specific routes, especially in combination with DNA fingerprinting to identify specific individuals that may have used the route. Scat detecting dogs can detect carnivore scats with a high degree of efficiency (Long et al. 2007a; Long et al. 2007b). With the long battery life possible with some of the newer camera trap models, camera-trap based detection studies can also be conducted in these corridors with minimal repeated field seasons. Similarly, GPS collars with low frequency fix rates can also run for years without field support and can result in detection of long-range dispersal movements across some of the important jaguar areas. Lastly, the importance of community knowledge about jaguar behavior and movement and recording actual instances of jaguars using specific routes in these corridor areas can significantly add to our understanding of jaguar connectivity. A combination of these measures, building on the results of this analysis, has the potential to inform jaguar conservation strategies and safeguard the long-term persistence of the species across the Americas.

References

Adriaensen, F., Chardon, J. P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003). The application of 'least-cost' modelling as a functional landscape model. *Landscape and urban planning*, *64*(4), 233-247.

Agresti, A. (2012). *Categorical data analysis* (Vol. 792). John Wiley & Sons.

Alvarenga, G. C., Chiaverini, L., Cushman, S. A., Dröge, E., Macdonald, D. W., Kantek, D. L. Z., Morato, R. G., Thompson, J. J., Oscar, R. B. L. M., Abade, L., de Azevedo, F. C. C., Ramalho, E. E., & Kaszta, Ż. (2021). Multi-scale path-level analysis of jaguar habitat use in the Pantanal ecosystem. *Biological Conservation*, *253*, 108900.

Athreya, V., Odden, M., Linnell, J. D., Krishnaswamy, J., & Karanth, U. (2013). Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PloS one*, *8*(3), e57872.

Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J., & Ericsson, G. (2011). A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology*, *80*(2), 466-476.

Burke, K. (2020). Conflicts and Attitudes Regarding the Return of the Grey Wolf to California. *Humboldt Geographic*, *1*(1), 18.

Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C., & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1578), 2642-2651.

Crooks K. R., Sanjayan M., (2006) Connectivity conservation: maintaining connections for nature. In: Crooks KR, Sanjayan M (eds) *Connectivity conservation*. Cambridge University Press, Cambridge, p 1.

Da Silveira, R., Ramalho, E. E., Thorbjarnarson, J. B., & Magnusson, W. E. (2010). Depredation by jaguars on caimans and importance of reptiles in the diet of jaguar. *Journal of Herpetology*, *44*(3), 418-424.

De La Torre, J. A., González-Maya, J. F., Zarza, H., Ceballos, G., & Medellín, R. A. (2018). The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar Panthera onca. *Oryx*, *52*(2), 300-315.

dos Santos Ramalheira, C., Bozzetti, B. F., da Cruz, A. D., Palmeirim, A. F., Cabral, M. M., & Rosas, F. C. (2015). First record of jaguar predation on giant otter (*Pteronura brasiliensis*). *Animal Biology*, *65*(1), 81-86.

D'Acunha, B., Dalmagro, H., Lathuilliere, M., Arruda, P., Couto, E., Brando, P., George V., & Johnson, M. (2021, December). How do carbon and water fluxes change with land use and land cover in the Amazon, Cerrado and Pantanal biomes? An analysis of eddy covariance data across the state of Mato Grosso. In *AGU Fall Meeting Abstracts* (Vol. 2021, pp. B13D-06).

Dickson, B. G., Albano, C. M., Anantharaman, R., Beier, P., Fargione, J., Graves, T. A., Gray, M. E., Hall, K. R., Lawler, J. J., Leonard, P. B., Littlefield, C. E., McClure, M. L., Novembre, J., Schloss, C. A., Schumaker, N. H., Shah, V. B., & Theobald, D. M. (2019). Circuit-theory applications to connectivity science and conservation. *Conservation Biology*, *33*(2), 239-249.

Diniz, M. F., Machado, R. B., Bispo, A. A., & Brito, D. (2018). Identifying key sites for connecting jaguar populations in the Brazilian Atlantic Forest. *Animal conservation*, *21*(3), 201-210.

Eisenberg, C., & Eisenberg, C. (2014). Jaguar (Panthera onca). *The Carnivore Way: Coexisting with and Conserving North America's Predators*, 217-240.

Eizirik, E., Kim, J. H., Menotti-Raymond, M., Crawshaw Jr, P. G., O'Brien, S. J., & Johnson, W. E. (2001). Phylogeography, population history and conservation genetics of jaguars (Panthera onca, Mammalia, Felidae). *Molecular ecology*, *10*(1), 65-79.

Fattebert, J., Robinson, H. S., Balme, G., Slotow, R., & Hunter, L. (2015). Structural habitat predicts functional dispersal habitat of a large carnivore: how leopards change spots. *Ecological Applications*, *25*(7), 1911-1921.

Gese, E. M., Terletzky, P. A., Cavalcanti, S. M., & Neale, C. M. (2018). Influence of behavioral state, sex, and season on resource selection by jaguars (Panthera onca): Always on the prowl?. *Ecosphere*, *9*(7), e02341.

Gilbert-Norton, L., Wilson, R., Stevens, J. R., & Beard, K. H. (2010). A meta-analytic review of corridor effectiveness. *Conservation biology*, *24*(3), 660-668.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote sensing of Environment*, 202, 18-27.

Haag, T., Santos, A. S., Sana, D. A., Morato, R. G., Cullen Jr, L., Crawshaw Jr, P. G., De Angelo, C., Di Bitetti, M. S., Salzano, F. M., & Eizirik, E. (2010). The effect of habitat fragmentation on the genetic structure of a top predator: loss of diversity and high differentiation among remnant populations of Atlantic Forest jaguars (Panthera onca). *Molecular Ecology*, *19*(22), 4906-4921.

Hayward, M. W., Kamler, J. F., Montgomery, R. A., Newlove, A., Rostro-García, S., Sales, L. P., & Van Valkenburgh, B. (2016). Prey preferences of the jaguar *Panthera onca* reflect the post-Pleistocene demise of large prey. *Frontiers in Ecology and Evolution*, *3*, 148.

Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecological modelling*, *199*(2), 142-152.

Jhala, Y. V., Qureshi, Q., & Nayak, A. K. (2019). Status of tigers, co-predators and prey in India 2018: Summary Report. *National Tiger Conservation Authority, New Delhi and Wildlife Institute of India, Dehradun*, *650*.

Johnson, W. E., Eizirik, E., & O'Brien, S. J. (2002). Evolution and genetics of jaguar populations: implications for future conservation efforts. *Jaguars in the new millennium: A status assessment, priority detection, and recommendations for the conservation of jaguars in the Americas*, 519-534.

Karandikar, H., Serota, M. W., Sherman, W. C., Green, J. R., Verta, G., Kremen, C., & Middleton, A. D. (2022). Dietary patterns of a versatile large carnivore, the puma (Puma concolor). *Ecology and Evolution*, *12*(6), e9002.

Lewis, J. (2022). leastcostpath: Modelling pathways and movement potential within a landscape (Version 1.8.7). R package version 1.8.7.

Long, R. A., Donovan, T. M., Mackay, P., Zielinski, W. J., & Buzas, J. S. (2007). Effectiveness of scat detection dogs for detecting forest carnivores. *The Journal of Wildlife Management*, *71*(6), 2007-2017.

Long, R. A., Donovan, T. M., Mackay, P., Zielinski, W. J., & Buzas, J. S. (2007). Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. *The Journal of Wildlife Management*, *71*(6), 2018-2025.

Manly, B. F. L., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2007). *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media.

Marrotte, R. R., & Bowman, J. (2017). The relationship between least-cost and resistance distance. *PloS one*, *12*(3), e0174212.

McClintock, B. T., Langrock, R., Gimenez, O., Cam, E., Borchers, D. L., Glennie, R., & Patterson, T. A. (2020). Uncovering ecological state dynamics with hidden Markov models. *Ecology letters*, *23*(12), 1878-1903.

McRae, B. H., Dickson, B. G., Keitt, T. H., & Shah, V. B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, *89*(10), 2712-2724.

McRae, B. H., Shah, V., & Edelman, A. (2016). Circuitscape: modeling landscape connectivity to promote conservation and human health. *The Nature Conservancy*, *14*, 1-14.

Medellín, R. A., de la Torre, J. A., Zarza, H., Chávez, C., & Ceballos, G. (2016). *El jaguar en el siglo XXI: la perspectiva continental*. Fondo de Cultura Económica.

Morato, R. G., Thompson, J. J., Paviolo, A., de La Torre, J. A., Lima, F., McBride Jr, R. T., Paula, R. C., Cullen Jr, L., Silveira, L., Kantek, D. L. Z., Ramalho, E. E., Maranhão, L., Haberfeld, M., Sana, D. A., Medellin, R. A., Carrillo, E., Montalvo, V., Monroy-Vilchis, O., Cruz, P., Jacomo, A. T., et al. (2018). Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics.

Newmark, W. D. (1987). A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature*, *325*(6103), 430-432.

Quigley, H., Foster, R., Petracca, L., Payan, E., Salom, R., & Harmsen, B. (2017). *Panthera onca* (errata version published in 2018). The IUCN Red List of Threatened Species 2017: e. T15953A123791436.

Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. *Biological conservation*, *143*(4), 939-945.

Roques, S., Sollman, R., Jácomo, A., Tôrres, N., Silveira, L., Chávez, C., Keller, C., Mello do Prado, D., Carignano Torres, P., Jorge dos Santos, C., Bernardes Garcia da Luz, X. Magnusson, W. E., Godoy, J. A., Ceballos, G., & Palomares, F. (2016). Effects of habitat deterioration on the population genetics and conservation of the jaguar. *Conservation genetics*, *17*, 125-139.

Rainey, M. (2009) Using graph theory to compare least cost path and circuit theory connectivity analyses. *BIO 515 Fall*. www.montana.edu/hansenlab/documents/labinstructions/Bio515Project

Rainey, M. M. (2012). *Validating alternative methods of modeling wildlife corridors using relocation data from migrating elk and dispersing wolverines*. Montana State University.

Ruiz-Garcia, M., Payán, E., Murillo, A., & Alvarez, D. (2006). DNA microsatellite characterization of the jaguar (Panthera onca) in Colombia. *Genes & genetic systems*, *81*(2), 115-127.

Sanderson, E. W., Redford, K. H., Chetkiewicz, C. L. B., Medellin, R. A., Rabinowitz, A. R., Robinson, J. G., & Taber, A. B. (2002). Planning to save a species: the jaguar as a model. *Conservation Biology*, *16*(1), 58-72.

Signer, J., Fieberg, J., & Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and evolution*, *9*(2), 880-890.

SOS Mata Atlântica (1998). Atlas da evolução dos remanescentes florestais e ecossistemas associados no domínio da Mata Atlântica no período 1990-1995. *Fundação SOS Mata Atlântica, São Paulo*.

Thompson, J. J., & Velilla, M. (2017). Modeling the effects of deforestation on the connectivity of jaguar *Panthera onca* populations at the southern extent of the species' range. *Endangered Species Research*, *34*, 109-121.

UNEP-WCMC & IUCN (2022). Protected Planet: The World Database on Protected Areas (WDPA), [December 2022], Cambridge, UK: UNEP-WCMC and IUCN. Available at: www.protectedplanet.net.

Viana, V. M. (1997). Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*, 351-365.

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A., & Watson, J. E. (2016). Global terrestrial Human Footprint maps for 1993 and 2009. *Scientific data*, *3*(1), 1-10.

Walker, S., Novaro, A., Hornocker, M., & Negri, S. (2010). The world's southernmost pumas in Patagonia and the southern Andes. *Cougar: ecology and conservation*, 91-102.

Wildlands Network. (2022, August 4). Arizona Jaguar "El Jefe" Reappears in Central Sonora. Wildlands Network. https://wildlandsnetwork.org/news/arizona-jaguar-central-sonora

Wultsch, C., Caragiulo, A., Dias-Freedman, I., Quigley, H., Rabinowitz, S., & Amato, G. (2016). Genetic diversity and population structure of Mesoamerican jaguars (*Panthera onca*): implications for conservation and management. *PloS one*, *11*(10), e0162377.

WWF. (2020). WWF Jaguar Strategy 2020-2030.

Zeller, K. A., Rabinowitz, A., Salom-Perez, R., & Quigley, H. (2013). The jaguar corridor initiative: a range-wide conservation strategy. *Molecular population genetics, evolutionary biology and biological conservation of neotropical carnivores. Nova Science Publishers, New York*, 629-658.

Zimmermann, A., Johnson, P., de Barros, A. E., Inskip, C., Amit, R., Soto, E. C., Lopez-Gonzalez, C. A., Sillero-Zubiri, C., de Paula, R., Marchini, S., Soto-Shoender, J., Perovic, P. G., Earle, S., Quiroga-Pacheco, C. J., & Macdonald, D. W. (2021). Every case is different: Cautionary insights about generalisations in human-wildlife conflict from a range-wide study of people and jaguars. *Biological Conservation*, *260*, 109185.

Concluding Remarks

This dissertation investigates animal space use and how environmental conditions affect space use and behavior at different scales. In Chapter 1, I study how vicuñas, typically known to maintain exclusive territories, extensively share space and demonstrate high tolerance for conspecifics from other vicuña families at our study site in the high Andes, results that can help inform conservation of the threatened southern subspecies of vicuñas, recently decimated due to an epidemic of mange, caused by mites *(Sarcoptes scabiei)*, with populations in the study site in SGNP, Argentina, having crashed by more than 99% (Donadio, E., unpublished data) since 2017. The disease spreads through direct contact (Curtis 2004), representing a significant threat for a social, sedentary species like the vicuña due to the role of animal density in disease transmission (Pence and Ueckermann 2002). Vicuñas, one of only two large ungulate species in this high Andean ecosystem, affect organisms across trophic levels. In addition to shaping the primary producer community and comprising a significant proportion of puma diets in the area, vicuñas and guanacos constituted 88% of the prey items in 183 condor pellets (Perrig et al. 2017). The importance of vicuñas in the ecosystem is emphasized by recent work that reports significantly decreased condor presence in the region after the vicuña population decline caused by mange (Monk et al. 2022). The results of this study may offer critical insights in the efforts for managed recovery of vicuña populations in an important part of their range. The tolerance of and frequent proximity to conspecifics from multiple distinct family groups represents a challenge in vicuña conservation from a disease management perspective. However, the sedentary nature of the species, and the tendency for high site fidelity, at least within family groups, offers opportunities to isolate populations in case of future epidemics. Two specific recommendations can be made based on the results of this study. First, urgent efforts need to be undertaken to identify undisturbed populations of the southern subspecies and assess the impact and extent of the recent mange epidemic on these populations. Second, the degree of connectivity and interactions within these undisturbed and other human-impacted populations needs to be mapped. Based on the results of these assessments, geographic areas within the subspecies' range that are critical for ensuring the long-term persistence of the species in the region can be identified and prioritized for conservation actions and legal protection measures.

In Chapter 2, I assess how landscape heterogeneity affects puma space use and movement across three sites in the high Andean and Patagonian steppes, and show that pumas limit space use and movement to small areas with increasing landscape homogeneity, with consequent implications on management of conflict between pumas and livestock owners in working landscapes. Understanding how predators interact with landscapes is important given the wide array of impacts these species can have on their surroundings beyond direct and indirect effects on food webs (Estes et al. 2011; Pauli et al. 2018). Additionally, ecosystems and physical landscapes are complex entities with a multitude of biotic and abiotic factors that affect each other, often creating a host of direct, indirect and cryptic interactions and positive and negative feedback loops that can regulate systems or move them into alternative steady states. Heterogeneity in landscapes, both in the form of variation in physical features and differences in species composition, adds to this complexity. As apex predators that exert top-down pressures on ecosystems, large carnivores may have important impacts on the landscape, creating positive feedback loops that may result in even more heterogeneity, especially in the mesoherbivore-dominated landscapes of southern South America (Monk and Schmitz 2022). Where predators

kill prey can affect local ecosystem dynamics in multiple ways, including increasing nutrient availability and disturbing vegetation at the site (Holtgrieve et al. 2009; Risch et al. 2020). While the specific landscape parameters at kill sites that predators select for during predation are important, the spatial distribution and clustering of these predation sites can also result in additional non-consumptive impacts such as the landscape of fear (Laundre et al. 2010) that can further increase heterogeneity due to avoidance of these sites by prey species. While this study assesses how landscape factors affect puma space use and movement, these differences in puma behavior are thus likely to transform the landscape themselves.

In Chapter 3, I use a large, publicly available jaguar location dataset to identify key corridor areas critical for maintaining connectivity between important jaguar populations and habitats across the range of the species in the Americas, and compare these corridors with previously identified movement routes for the species (Rabinowitz and Zeller 2010; Zeller et al. 2013). The identified areas can be the focus of intensive ground-truthing and validation studies that can help confirm jaguar use and movement through them. Additionally tools such as genetic analysis can contribute towards understanding the viability of these identified corridors that can eventually inform jaguar conservation strategies and help focus conservation efforts for the long-term persistence of the species, currently facing several significant threats across its range (De La Torre et al. 2018).

References

Curtis, C. F. (2004). Current trends in the treatment of Sarcoptes, Cheyletiella and Otodectes mite infestations in dogs and cats. *Veterinary Dermatology*, *15*(2), 108-114.

De La Torre, J. A., González-Maya, J. F., Zarza, H., Ceballos, G., & Medellín, R. A. (2018). The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar Panthera onca. *Oryx*, *52*(2), 300-315.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter et al. (2011). Trophic downgrading of planet Earth. *Science*, *333*(6040), 301-306.

Holtgrieve, G. W., Schindler, D. E., & Jewett, P. K. (2009). Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. *Ecological Research*, 24(5), 1125-1135.

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal*, 3(1).

Monk, J. D., & Schmitz, O. J. (2022). Landscapes shaped from the top down: predicting cascading predator effects on spatial biogeochemistry. *Oikos*, 2022(5), e08554.

Monk, J. D., Smith, J. A., Donadío, E., Perrig, P. L., Crego, R. D., Fileni, M., Bidder, O., Lambertucci S. A., Pauli J. N., Schmitz O. J., & Middleton, A. D. (2022). Cascading effects of a disease outbreak in a remote protected area. *Ecology Letters*, *25*(5), 1152-1163.

Pauli, J. N., Donadio, E., & Lambertucci, S. A. (2018). The corrupted carnivore. *Ecology*, *99*(9), 2122-2124.

Pence, D. B., & Ueckermann, E. (2002). Sarcoptic mange in wildlife. *Revue scientifique et technique (International Office of Epizootics)*, *21*(2), 385-398.

Perrig, P. L., Donadio, E., Middleton, A. D., & Pauli, J. N. (2017). Puma predation subsidizes an obligate scavenger in the high Andes. *Journal of Applied Ecology*, *54*(3), 846-853.

Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca. Biological conservation*, *143*(4), 939-945.

Risch, A. C., Frossard, A., Schütz, M., Frey, B., Morris, A. W., & Bump, J. K. (2020). Effects of elk and bison carcasses on soil microbial communities and ecosystem functions in Yellowstone, USA. *Functional Ecology*, 34(9), 1933-1944.

Zeller, K. A., Rabinowitz, A., Salom-Perez, R., & Quigley, H. (2013). The jaguar corridor initiative: a range-wide conservation strategy. *Molecular population genetics, evolutionary biology and biological conservation of neotropical carnivores. Nova Science Publishers, New York*, 629-658.