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A marine subsidy reshapes the ecology of a large terrestrial carnivore

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Efforts to restore wildlife populations are increasing worldwide, yet many of these initiatives take place amidst significant ecological change. In altered ecosystems with novel species compositions, returning wildlife may alter their behaviours and interactions with other species. In Patagonia, the extirpation of terrestrial predators following European colonization, including the puma, facilitated the establishment of Magellanic penguin colonies along Argentina's coast. Recently, the creation of a national park in coastal Patagonia has fostered the recovery of pumas and resulted in an unexpected predator–prey relationship between pumas and penguins. Using a suite of animal movement metrics and generalized spatial mark–resight models, we tested how access to penguins affects puma behaviour and abundance. Consistent with the resource dispersion hypothesis, pumas responded to the availability and abundance of penguins by increasing their site fidelity when penguins were present but ranging more widely when the penguins migrated out of the park. This behavioural adaptation led to frequent encounters among pumas, suggesting greater social tolerance. Further, the park now supports the highest density of pumas recorded to date. Our work adds to a rapidly growing body of literature suggesting that the restoration of large carnivores in novel ecosystems can lead to novel interactions that transform their behaviours.

1. Introduction

Wildlife restoration, through the establishment of protected areas, targeted reintroductions and the development of wildlife corridors, is increasingly used worldwide to combat biodiversity declines [1–5]. The importance of restoring wildlife populations is reflected in ambitious conservation initiatives and international agreements, such as the Convention on Biological Diversity, the United Nations Environment Programme, 30 × 30 and the UN Decade on Restoration (2021–2030) [2,6–8]. A central objective of these efforts is to restore key trophic interactions that can shape the structure and function of ecosystems, including herbivory, predation, and scavenging [6,9–11]. However, as wildlife restoration efforts increasingly underpin global conservation strategies, it is crucial to take into consideration that species are returning to ecosystems that have changed significantly since their extirpation [12]. These novel ecosystems, now influenced by novel species compositions, human infrastructures and climates, can reshape the resulting trophic interactions of returning wildlife [13–15].

Through predation and wide-ranging movements, large carnivores can exert top-down pressure on ecosystems by regulating prey populations, shaping prey behaviour such as herbivory, and driving nutrient transport and deposition [16]. Due to these widespread ecosystem effects, the restoration of large carnivore populations has been a particular focus of global conservation efforts [16–19]. Although some studies support the predicted ecological effects of restoring large carnivores, other recent studies suggest that these impacts are often absent or weaker than anticipated [12,16,19,20]. For instance, the famous reintroduction of wolves (*Canis lupus*) to the Greater Yellowstone Ecosystem and recovery of wolves across Europe failed to consistently bring about the expected large-scale effects on prey populations and the restoration of plant communities [19,21–24]. A potential reason for these inconsistent effects is that predator restoration is occurring in ecosystems that have been altered. Changes to prey and vegetation communities, along with human-modified landscapes, may affect when, where and how predators obtain food, ultimately shaping their ecological impact. Thus, there is a need to first understand how novel ecosystems modify the behaviours of returning large carnivores.

Here, we assess how access to a novel prey resource of Magellanic penguins (*Spheniscus magellanicus*) impacts a recovering puma population in coastal Patagonia. Following the European settlement of Patagonia during the twentieth century, pumas, foxes (*Lycalopex griseus* and *Lycalopex culpaeus*) and several herbivores, including guanacos (*Lama guanicoe*) and rheas (*Rhea pennata*), were largely extirpated to accommodate sheep ranching [25,26]. The eradication of pumas and other mainland predators appears to have triggered the expansion of Magellanic penguin colonies, formerly restricted to islands off the Atlantic coast of Argentina [27,28]. More recently, conservation efforts have begun to establish protected areas to restore pre-settlement wildlife to Patagonia [26,29]. One such protected area is Monte León National Park (MLNP), a former ranch that was donated to the Argentinian Park Service in 2004 and is home to a breeding colony of Magellanic penguins (approximately 40 000 breeding pairs) [30]. Shortly after MLNP was created, Magellanic penguin remains were found in puma scats, and pumas were frequently detected in the colony, marking the first documentation of this interaction [31,32] (electronic supplementary material, video S1). Yet little is known about how this interaction impacts puma behaviour.

The resource dispersion hypothesis [33], which suggests that the availability and distribution of resources drive consumer behaviour, can be used to predict how an abundant and concentrated resource might impact pumas at MLNP. In MLNP, Magellanic penguins are abundant but confined to a small breeding colony along the coast, spending just over half the year on land to breed from September to April (figure 1). Thus, based on the resource dispersion hypothesis, we predicted that pumas would adapt to this spatially constrained and abundant resource in three ways: (i) penguin-hunting pumas would increase their site fidelity, reduce movement and aggregate at the penguin colony when penguins were present, (ii) because the cost of sharing an abundant resource is low, penguin-hunting pumas would increase their social tolerance of conspecifics, and (iii) the abundance of prey, including but not limited to penguins, would lead to a high density of pumas in the park. To test these predictions, we first analysed a dataset of GPS-collared pumas, assessing their movement patterns and social interactions in the presence and absence of penguins [34]. We then integrated GPS collar data and a camera trap array throughout the park to estimate puma density [35,36].

2. Methods

(a) Study area

We conducted our fieldwork at MLNP, located in Santa Cruz province in southern Argentina, from September 2019 to January 2023 (figure 1). The park lies at an elevation of 0–350 m above sea level and receives approximately 250 mm of precipitation annually. With a total area of 610 km^2, MLNP is characterized by a coastal steppe ecosystem comprising both shrubland and grassland habitats [37].

Pumas are the lone large carnivore in the region. As generalist predators, pumas have been found to have a wide variety of biotic interactions and prey on as many as 232 different species, ranging from elk (*Cervus canadensis*) to desert tortoise (*Gopherus agassizii*) [38,39]. The park is home to a substantial population of guanacos, rheas and exotic European hares (*Lepus europaeus*), the typical prey species of pumas in the region [26]. Notably, the park contains 30 km of coastline, including a 2 km stretch that serves as a breeding colony for approximately 40 000 breeding pairs of Magellanic penguins [30].

(b) Monitoring puma movement

To monitor the movement of pumas in MLNP, we deployed GPS collars (Lotek Iridium Track M2D) on 14 adult pumas between September 2019 and December 2023, including nine females and five males (electronic supplementary material, table S1). All GPS collars were programmed to acquire location data at a 3 h interval. Fieldwork was conducted on permit no. DRPA 162 and subsequent renewals issued by Administración de Parques Nacionales (APN), Argentina.

(c) Describing puma diet

We described puma diets by investigating individual puma GPS clusters. We defined GPS clusters as any two or more points for the same puma within 20 m of each other over a 36 h period [40]. Field teams investigated a subset of clusters by conducting systematic searches to identify kill sites over a series of dedicated field seasons between September 2019 and January 2023. Clusters were investigated within 30 days of their first recorded locations. At the investigated clusters, prey remains such as hair, skin, stomach contents and bone fragments were used to identify the prey species. Based on confirmed penguin kills at clusters, pumas were subsequently classified as either pumas that predate penguins or not (electronic supplementary material,

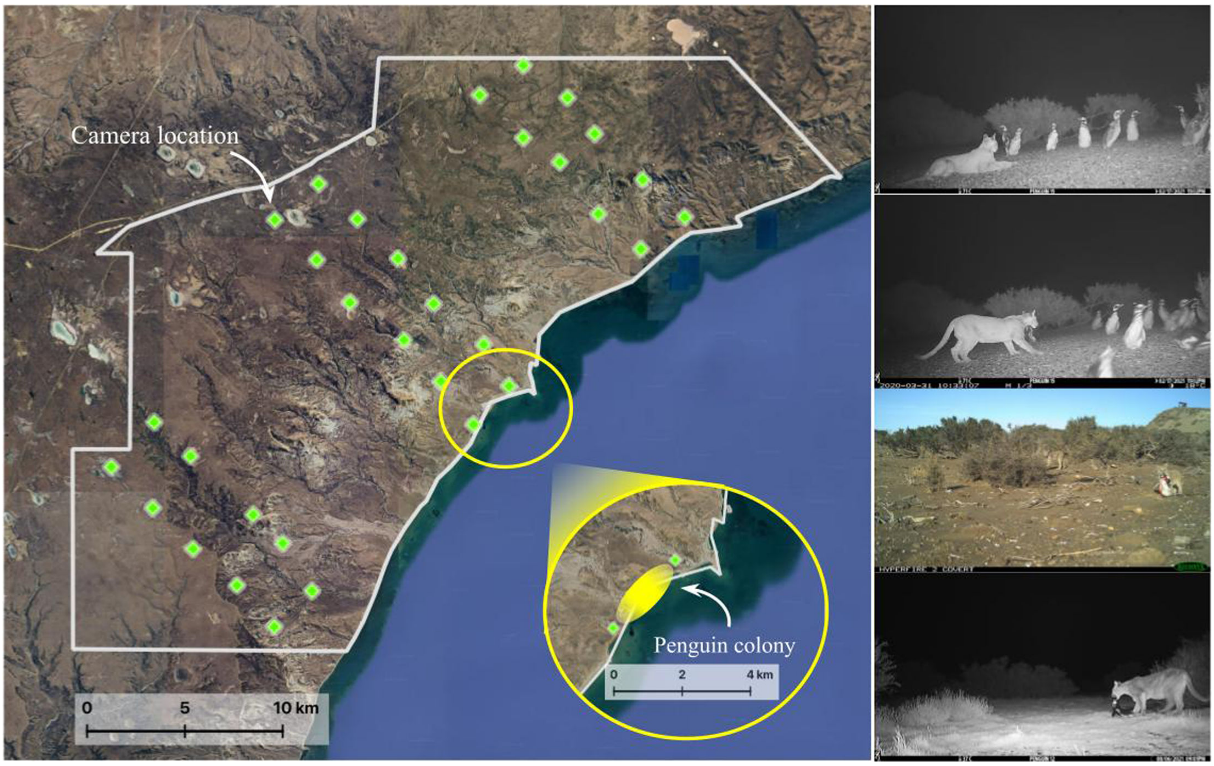

Figure 1. Location of camera trap grid at Monte León National Park (white-lined polygon), Santa Cruz province, Argentina, June 2020–December 2022. The yellow highlight in the inset map indicates the location of the single penguin colony in the park. Camera trap photos show puma and penguin interactions within the colony.

table S1). GPS clusters are generally biased against detecting small prey like penguins [41]. Therefore, this methodology was used to identify pumas that have consumed penguins at least once, not to quantify the extent to which they killed penguins.

(d) Movement metrics by diet

Following the protocol of Abrahms *et al.* [34], we calculated five movement metrics to describe the patterns of movement for pumas with different diets across seasons (i.e. defined by the presence and absence of penguins in the park). To compare between seasons, we split the GPS data for individual pumas while penguins were present (October–April) and absent (June–August). We omitted the months of May and September, which were two months of transition when penguins were either arriving to breed or leaving to migrate. For each period per individual, we used a random subset of three months since the penguins are only completely absent from the park for a three month period. For individuals that were monitored for over a year, we treated each year of monitoring as separate (referred to as a puma year) to account for changing behaviours between years of study. For each puma year and season, we estimated (i) mean turn angle correlation (the degree of similarity in directional changes from one relocation to the next), (ii) mean residence time (the number of hours an individual spent inside a predefined polygon over a predefined period of time), (iii) mean time to return (the number of hours an individual spent before returning to a predefined polygon), (iv) mean volume of intersection (overlap between monthly home ranges derived from the three month subset on a scale from 0 to 1), and (v) maximum net squared displacement from the penguin colony (max NSD, calculated as the largest squared straight-line distance between the centroid of the penguin colony and any other point during the three month timeframe) [34,42]. Monthly home ranges were calculated using the *ctmm* package (v. 1.2.0), following the model-based framework described by Calabrese et al. [43], which analysed animal movement data as a continuous-time stochastic process. The best-fit models were then used to generate 95% autocorrelated kernel density (AKDE) home ranges [44,45]. Max NSD and mean turn angle correlation (the sum of squares of distances between n successive turn angles) were calculated using the package *amt* v. 0.1.7 [46]. For mean residence time and mean time to return, the radius of the predefined polygon was set equal to 2× mean step length with a cut-off time of 12 h [34]. We used 12 h to capture consecutive visits to the penguin colony. Mean residence time, mean time to return and mean volume of intersection were calculated using *adehabitatLT* v. 0.3.27 and *adehabitatHR* v. 0.4.21 [47]. Finally, we used linear mixed-effects models to compare variation in each movement metric with each group (diet and season) as a fixed effect and puma year as a random effect. We then used least squares means and pairwise post hoc comparisons to quantify differences between groups using the package *emmeans* v. 1.5.2.1 [48].

To further test the site fidelity of pumas that predated penguins to the penguin colony, we calculated the number of returns to a previously visited area (i.e. revisitations) for each puma year. We defined a revisit as a relocation within a radius of 2× the average step length of a previously visited location after the individual had left that location for over 12 h [34]. Again, we used 12 h to capture consecutive visits to the penguin colony. All revisits were calculated using the package *recurse* v. 1.1.2 [49]. Because pumas that did not predate penguins were not recorded within 1 km of the penguin colony (electronic supplementary material, table S1), analyses were restricted to individuals that predated penguins. To overcome the effect of overdispersion in the count data, we then used negative binomial regression models to compare the variation in revisitations with distance to the penguin colony as a main effect and puma year as a random effect for each season.

(e) Puma social tolerance by diet

To examine puma social tolerance by diet, specifically between individuals that predated penguins and those that did not, we defined puma interactions as simultaneous relocation data (GPS locations with the same timestamp) from any two individual pumas at less than or equal to 200 m from each other. We used 200 m as our threshold for consistency with previous studies looking at puma interactions [50]. Individuals needed to separate from each other for more than 12 h before we counted another interaction. Again, we used a 12 h threshold to account for daily visits and therefore, repeated encounters with conspecifics. Since each individual was monitored for different periods of time, we then calculated a weekly contact rate for each individual. We then fit a linear regression model with contact rate as the response variable and diet type as the fixed effect.

Next, we tested whether interactions occurred more frequently near the penguin colony using logistic regressions with a used versus availability framework. We generated 10 random points for each puma interaction within the 95% kernel density estimation for all sampled pumas. We used the package *lme4* v. 1.1.33 in R to run univariate logistic regressions with the used and available points as the response variable and distance to the penguin colony as the covariate [51].

(f) Estimation of puma density

In 2020, we established a camera trap grid of 32 cameras (Reconyx Hyperfire 2) spanning from the coast to the park border (figure 1). We used a clustered array design, with cameras spaced 3 km apart, to maintain spatial representation throughout the park while allowing for easier field implementation compared with regular spacing [52]. We visited each camera approximately every three months to check batteries and download data. To facilitate puma identification, each camera was set to take a burst of three photos when triggered. We sorted photos of pumas by whether individuals were wearing GPS collars and cross-referenced each image with the corresponding GPS locations to aid in individual identification. All other photos of pumas were sorted as ‘unmarked’. We used the program *DigiKam* to tag all of the photos. Detections separated by more than 30 min from the next detection were considered to be independent [36]. The animal encounter data were split into 1 day occasions for a density model when the penguins are present from 1 October to 31 December 2022, and 1 day occasions for a separate density model when the penguins are absent from 1 June to 31 August 2022.

To estimate the density of pumas in MLNP, we integrated a generalized spatial mark–resight model (gSMR) using both camera trap and GPS collar data [36,53,54]. Spatial mark–resight models (SMR) estimate the density of individual activity centres by modelling the encounter histories of marked animals across space as a Poisson process with detections based on a baseline probability of resighting (λ) and space use (σ) that informs the decline of detection probability over increasing distance from individual activity centres. These detection parameters then also inform the process of estimating individual activity centres from the spatial counts of unmarked individuals as a Poisson process. Together, these sub-models estimate the total number of both encountered and unencountered individuals and their activity centres across the study area for an estimate of total population density. gSMR models are a subset of SMR models that can mitigate the bias introduced from the variation in camera detection rates for individuals that are marked (e.g. captured near the detector array [54]). We incorporated GPS data from the marked individuals to inform the location of the activity centre of collared individuals, the space use parameter (σ) in the detection function and baseline resighting/detection rate (λ). To reduce temporal autocorrelation, we used the *ctmm* package to estimate the effective sample size of GPS locations for each individual and then randomly subsampled that number of locations per puma [36].

We used Markov chain Monte Carlo (MCMC) to draw samples from the posterior distributions for each parameter of interest. We used the R package ‘NIMBLE’ v. 1.0.0 [55]). For each model, we ran three chains consisting of 50 000 iterations per chain and discarded the first 15 000 as burn-in. We assessed model convergence by visually inspecting trace plots and ensuring the *Rhat* values were less than 1.1 [56]. For all parameters, we calculated the 95% highest posterior density intervals and the 95% Bayesian credible intervals [57].

3. Results

(a) Movement metrics

Analysis of the puma movement metrics revealed differences by season and diet (figure 2; electronic supplementary material, table S2). Pumas that predated penguins had more variable movement patterns between seasons. Specifically, individuals that predated penguins had significantly larger home ranges when penguins were absent, with an average size twice as large during that period ($p > 0.01$; electronic supplementary material, table S2). Additionally, pumas that predated penguins exhibited a 25% increase in monthly volumetric intersection when penguins were present ($p > 0.01$; electronic supplementary material, table S2). Furthermore, pumas that predated penguins had an average residence time of 10 h longer and a time to return of 50 h shorter when penguins were present ($p > 0.01$ in both cases; electronic supplementary material, table S2). Finally, pumas that predated penguins had a maximum NSD when penguins were absent, which was nearly twice the size of all treatment groups ($p < 0.01$). In contrast, for individuals that did not predate penguins, there was no significant difference in each movement metric between seasons ($p > 0.05$). Furthermore, there were no significant differences between diet or season for turning angle correlation ($p > 0.05$ in both cases; electronic supplementary material, table S2).

(b) Site fidelity

The analysis of revisitations suggested a high site fidelity to the penguin colony (figure 3). Individuals that predated penguins had significantly more revisitations near the penguin colony both while penguins were present (estimate = -2.26×10^{-4}, 95% CI = -2.3×10^{-4} to -2.2×10^{-4}, $p < 0.01$) and absent (estimate = -1.03×10^{-4}, 95% CI = -1.1×10^{-4} to -9.9×10^{-5}, $p < 0.01$).

(c) Social interactions

We identified 295 puma–puma encounters from September 2019 to January 2023 between 14 individuals (electronic supplementary material, table S3; figure 4). There were 254 encounters between individuals that both predated penguins, 37 encounters between individuals with mixed diet types and four encounters between pumas that did not predate penguins. Most encounters were between two females ($n = 179$) or between a male and female ($n = 112$; figure 4). Only four encounters were between two males. Pumas that predated penguins had an average contact rate of 0.43, nearly 5× higher than those that did not predate penguins, which had an average contact rate of 0.09 (coefficient estimate = 0.33, 95% CI 0.12–0.54, $p < 0.01$; electronic supplementary material, table S3). Most contacts were within 1 km of the penguin colony ($n = 185$ or 63%) and were significantly more likely to occur near the penguin colony (estimate = -2.4×10^{-4}, 95% CI = -2.3×10^{-4} to -1.8×10^{-4}, $p < 0.001$). Finally, of the contacts within 1 km of the penguin colony, 131 (71%) were between two females.

(d) Puma density estimation

We obtained 110 independent photos of pumas (19 marked, 91 unmarked) in June–August while penguins were absent and 143 independent photos of pumas (29 marked, 114 unmarked) in October–December while penguins were present. The number of GPS points used in the puma density estimation model (quantified using the effective sample size) ranged from 27 to 131 GPS points. The estimated mean puma density was 13.3 ± 2.2 individuals per 100 km^2 (95% CRI 8.6–16.1) when penguins were absent and 13.2 ± 2.3 individuals per 100 km^2 (95% CRI 8.4–16.6) when penguins were present (electronic supplementary material, table S4). Gelman–Rubin statistics (R-hat) for the density model were <1.1 for all parameters, and visual inspections of trace plots indicated that the Markov chains successfully converged (electronic supplementary materials, figures S1–S8).

4. Discussion

Here, we showed that a breeding colony of Magellanic penguins strongly influenced the movement and spatial behaviour of a recovering puma population. According to the resource dispersion hypothesis, abundant and concentrated resources should result in more localized movements, greater sociality and higher population densities of predators. Pumas that predated penguins had concentrated movements and increased encounters with other individuals around the penguin colony. In addition to the remarkable flexibility that we observed in puma movement patterns and sociality, we documented the highest puma population density to date in the species' range [58]. Together, these findings highlight how a novel prey source is shaping the behaviour of this puma population, raising the possibility that such behavioural shifts could influence the ecological role of pumas and, in turn, affect the restoration of this coastal landscape.

Monte León National Park is a clear example in which an altered food web drives the behaviour and movement of an apex predator. Our study revealed that pumas that predated penguins adopted distinct movement strategies, highlighted by increased site fidelity, reflected in high residence time, shorter time to return, higher monthly volumetric intersection and frequent revisitation of the penguin colony. Pumas that prey on larger species, like guanacos, are already expected to have high residence times since larger prey can take multiple days to consume [59]. Therefore, the similarly high residence time observed for pumas that predate penguins is particularly noteworthy, as it suggests that penguins, despite being smaller prey, represent a highly valuable and accessible resource. Resource availability and diet can strongly shape movement patterns within species and populations. Orcas (*Orcinus orca*), for example, exhibit distinct movement patterns based on their target prey, adopting residency and large social groups when preying on salmon and displaying transient behaviour and smaller social groups when targeting migratory pinnipeds [60,61]. When penguins are absent from the study area, puma movement patterns shift dramatically. Displacement distance from the penguin colony increases, suggesting wider searches for food. Interestingly, individuals still frequently revisit the colony when penguins are absent, possibly awaiting their return or scavenging penguin remains. In fact, once the penguins left MLNP, one individual puma left the park for another penguin colony 45 km away. Although we classified diet as a binary variable due to sample size limitations, variation likely exists in the extent to which individual pumas prey on penguins, which could further explain the differences in movement metrics we observed. Future research should explore how this gradient in penguin colony use shapes spatial behaviour. In general, the costs and benefits associated with different movement strategies for wildlife may change over time, continuously influenced by food availability, breeding opportunities and predation risk. Our research suggests a deeper interplay between diet variation within populations and movement patterns than previously appreciated, and in particular, that diet in altered food webs can have widespread effects on predator behaviour.

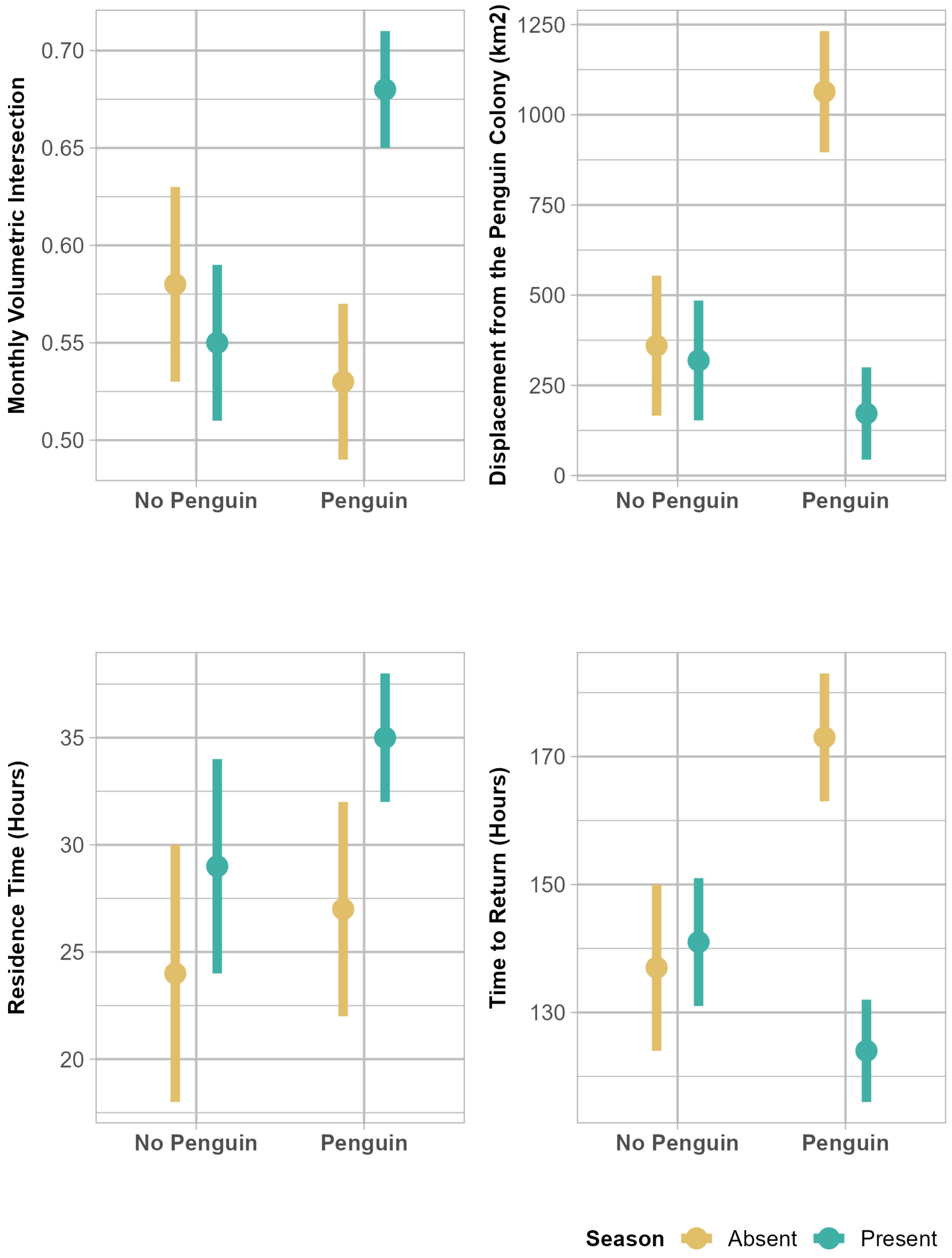

Figure 2. Means and standard deviations of four puma movement metrics (home range stability measured as monthly volumetric intersection, max net squared displacement (NSD) from the penguin colony, residence time and time to return) with significant differences by diet (i.e. penguins versus no penguins) and season (i.e. penguins absent versus penguins present), Monte León National Park, Argentina, September 2019 to January 2023.

In addition to changes in individual movement, the altered resource dynamics at MLNP has given rise to increased sociality between pumas. Historically, conspecific interactions were considered relatively rare for pumas and restricted mainly to breeding behaviour [62]. Generally speaking, females establish and defend home ranges that secure prey resources for both themselves and their kittens, while males establish and defend home ranges that provide access to multiple females [62]. Here, we found that conspecific interactions were more frequent among pumas that predated penguins, with the penguin colony acting as a spatial anchor for these interactions. Specifically, compared with pumas that did not predate penguins, penguin-hunting pumas were nearly five times more likely to encounter conspecifics, primarily other females, in this resource-rich environment. The increased encounter rate may in part reflect a rise in puma density at MLNP, yet the persistence of multiple individuals using the colony suggests that increased tolerance, rather than avoidance, facilitates this behaviour. These findings corroborate recent research that found high overlap of puma home ranges in areas with high prey density and the sharing of carcasses between individuals [50,63]. Yet, in contrast to our findings, previous studies primarily documented interactions at kill sites between males and females involving mutual exchange, such as food sharing with the expectation of future reciprocation, which seems unlikely in our population where penguins are small, abundant and easily captured, eliminating the need to share carcasses [64]. Our collar data are sex biased towards females, which may limit our ability to fully capture the sex

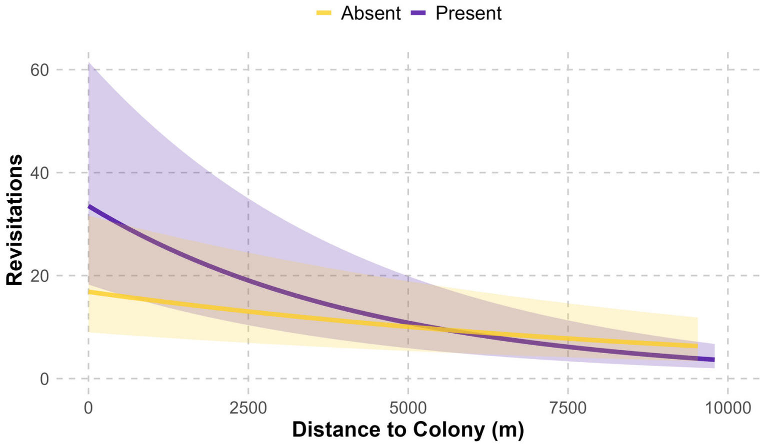

Figure 3. Negative binomial regression model output with confidence intervals for puma revisitations across individuals that predated penguins by distance to the penguin colony by season (i.e. penguins absent versus penguins present). Monte León National Park, Santa Cruz, Argentina, September 2019 to January 2023.

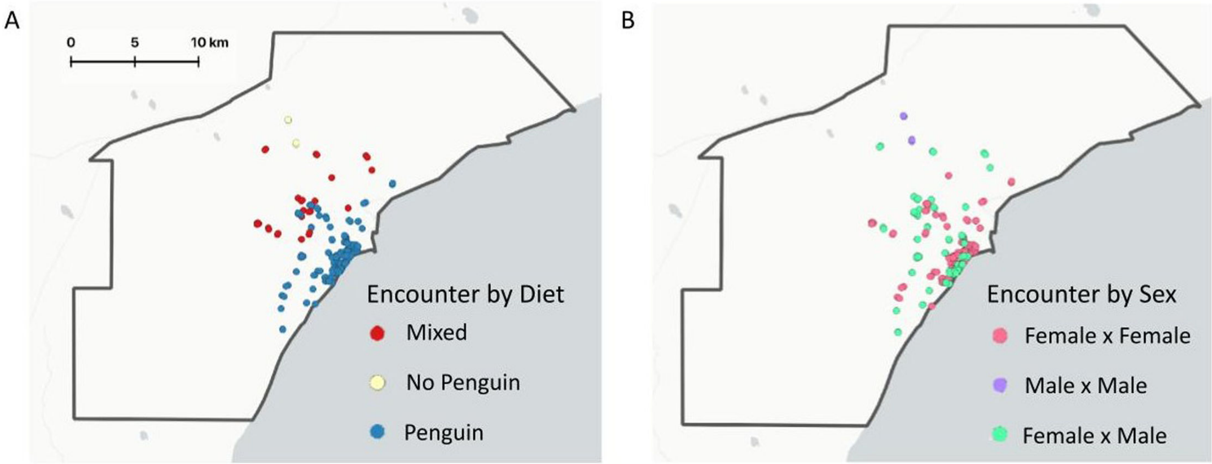

Figure 4. Locations of puma–puma encounters in MLNP, Argentina, September 2019 to January 2023. (A) Differences in colours represent the combined diet type of each individual. (B) Differences in colours represent the sex of each individual in a given encounter.

dynamics of these interactions. However, individuals at MLNP, particularly females, appear to relax territoriality and increase their tolerance for each other near the colony. Without testing for genetic relatedness, we cannot rule out the kinship hypothesis, which suggests a fitness benefit for tolerating related individuals [65]. Throughout the study period, we did observe numerous occasions in which mothers brought their kittens to forage in the penguin colony. Still, given the numerous individuals that use the colony, it is unlikely that the kinship hypothesis can fully explain this phenomenon. Furthermore, our collar data are sex biased towards females, so there may be other sex dynamics that we have not fully captured. Elsewhere, there is increasing research showing that other supposed solitary carnivores, like brown bears and jaguars, relax territoriality in environments with high prey densities [66,67]. Resource availability and prey characteristics can profoundly shape the movement ecology of large carnivores, and our results emphasize the need to better understand how novel environments will impact the movement of recovering large carnivores.

Monte León National Park presents a unique case study where an abundance of novel prey items appears to have contributed to a high-density predator population. The extreme abundance of prey within the park appears to facilitate a population-level response, culminating in a puma density far exceeding all previously reported estimates, according to a recent review [58]. Depending on specific methodological choices, density estimates can vary, and Murphy *et al.* [58] issued corrected density estimates for previous estimates that were not spatially explicit and/or included dependent individuals like kittens and juveniles [58]. Across these corrected densities, the 95th percentile for puma density was 3.7 independent pumas per 100 km^2, and the highest documented density was in the Chaco region of Bolivia at 5.7 independent pumas per 100 km^2 [58,68]. Within Argentina specifically, previous estimates of puma density have ranged from 0.2 to 4.3 individuals per 100 km^2. At 13.2 independent pumas per 100 km^2, the density estimate for pumas at MLNP is 2.3 times higher than the previously highest density estimate of pumas.

While an abundant, defenceless prey resource like Magellanic penguins is a clear outlier compared with previous puma density estimates, the penguin colony at MLNP may not be the sole contributor to the high puma population density. In addition to penguins, the park supports populations of other known puma prey species, such as guanacos, rheas and European hares, and is free from hunting—a strong regulator of puma populations across their range [69–72]. Among these prey species, guanacos occur at a relatively high density in our study area, with recent estimates indicating 18.9 individuals per km^2 [73]. Consistent with this, estimated puma density remained nearly identical during periods when penguins were present and when they were absent. This contrasts with other studies in which seasonal resource pulses only lead to temporary increases in predator density during peak prey availability [74]. Such findings suggest that the broader prey base in the park, particularly the high guanaco density, can support this puma population year-round.

Still, the extraordinarily high density of puma likely arose in part due to the penguin colony. Around the world, marine resources have led to hyperabundant populations of wolves, bears, jaguars and coyotes [66,75,76]. When resources are concentrated at a single point source, like the penguin colony at MLNP, a high density of pumas is dependent on the benefit of sharing the resource outweighing the cost of defending it [77]. Interestingly, this pattern resembles the behaviour of grizzly bear populations, which aggregate and tolerate one another at salmon runs or army cutworm moth (*Euxoa auxiliaris*) sites—a phenomenon not previously observed in pumas. Building on research of grizzly bears and other carnivores that tolerate high densities of conspecifics, future studies could test whether pumas use comparable behavioural strategies, including avoidance by females with cubs, when foraging at resource hotspots.

The restoration of wildlife to altered ecosystems presents unique challenges for conservation and management and engenders questions about the ultimate objectives and evaluation of restoration efforts. Yet, better understanding the mechanisms that drive novel interactions in recovering wildlife populations can help managers anticipate future challenges and tailor restoration strategies to local conditions. The restoration of predator populations is often predicated on widespread ecosystem benefits from the impacts predators have on prey behaviour and populations. However, many predator restorations have fallen short of anticipated widespread ecological impacts, in part due to the complexities of novel ecosystems. Our study provides a compelling example, where the establishment of a protected area facilitated a novel predator–prey dynamic that led to unanticipated ecological outcomes. Despite predation by pumas, recent surveys suggest that the penguin population at MLNP is increasing [30]. At MLNP, the impact of pumas on the behaviour and population of guanacos, the primary large herbivore in the region and the consequent effects on the park's vegetation community remain unanswered. Importantly, the presence of penguins in the park overlaps with the birthing season for guanacos, offering a potential reprieve from predation for guanacos during this critical period. The guanaco population at MLNP occurs at relatively high density, suggesting that the increase in puma density may not have strong numerical effects. However, guanaco behaviour, particularly in areas near the penguin colony where puma activity is concentrated, may be influenced by elevated predation risk. It is clear that this altered food web is greatly impacting puma behaviour and density, but future research should investigate whether the addition of this novel prey has modified ecological interactions among pumas, guanacos and plants.

Ethics. The research was conducted under permit no. DRPA 162 issued by Argentina's Administracion de Parques Nacionales.

Data accessibility. The data used in this study are available on Zenodo [78].

Supplementary material is available online [79].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.W.S.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft, writing—review and editing; T.C.: formal analysis, methodology, writing—review and editing; W.X.: visualization, writing—original draft, writing—review and editing; P.A.E.A.: data curation, funding acquisition, investigation, methodology, project administration, writing—review and editing; E.D.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, writing—review and editing; A.D.M.: conceptualization, funding acquisition, investigation, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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