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Research Article

Carnivorous mammal assemblage and activity patterns associated with the invasion of *Acacia melanoxylon* R. Br. in the Tandilia Mountain System, Argentina

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Abstract

The replacement of grasslands with monospecific forests of Australian acacia (*Acacia melanoxylon*) has led to significant changes in habitat structure across the landscapes of Buenos Aires, Argentina, particularly in the Tandilia Mountain System. Given that this invasive tree drastically modifies plant architecture in these mountain grasslands, it is expected to affect the presence and habitat-use patterns of native fauna. We predicted a lower frequency of native carnivorous mammals in areas invaded by exotic acacia compared to native grasslands/scrub environments. To test this prediction, mammal presence was assessed using camera traps (photo-trapping) in the Paititi Private Natural Reserve, located within the Tandilia Mountain System. Throughout four seasonal samplings spanning one year, we evaluated the environmental use and daily activity patterns of two dominant mammalian predators: the Pampas gray fox (*Lycalopex gymnocercus*) and the Geoffroy's cat (*Leopardus geoffroyi*). While both species showed preferences towards areas with higher vegetation cover, no preferences were observed regarding the occupation of grassland/scrub environments compared to acacia forests. Regarding activity patterns, the fox was found to be more crepuscular/nocturnal. At the same time, the cat did not exhibit a clear activity pattern, being potentially active at any time of the day. The ecological flexibility may explain why they were not significantly affected by habitat changes in the studied area. Additionally, the remaining patches of native habitat in the region may help mitigate the effects of anthropogenic impact.

Introduction

Biological invasions constitute one of the main global environmental issues due to their profound impact on ecosystems (Vitousek et al., 1996). Some invasive species have altered ecosystems by modifying their ecological characteristics in an unprecedented way, leading to environmental deterioration and biodiversity loss (Charles and Dukes, 2007; Isbell et al., 2023).

Grasslands are one of the most widespread vegetation types on the planet (Bilenca and Miñarro, 2004). Their high soil productivity has made them a target for intense agricultural activity, leading to their replacement or degradation over recent decades. Consequently, the remaining grassland patches face increasing threats from invasive species, further compounding conservation challenges (Zalba and Villamil, 2002).

In Argentina, the Pampas region consists of a vast plain originally dominated by tall grasslands, where the introduction and rapid proliferation of cattle and horses led to a replacement of the tall grasses' physiognomy with short grasses. Pampas' landscape is formed by parcels with different land uses, with large areas being utilized for crops and grazing, rural settlements, and towns (Baldi et al., 2006). However, the proportion of land that can be dedicated to crops or grazing fields depends on soil quality or suitability, so areas unsuitable for these purposes, such as rocky, saline, or sandy soils, remain dominated by native grasslands (Viglizzo et al., 2001; Baldi et al., 2006).

Within the Pampas region, the Tandilia Mountain System has remained a biodiversity refuge for flora and fauna and a provider of ecosystem services, contrasting with the surrounding grassland areas, as its rocky soils prevent agricultural expansion (Vignolio et al., 2021). However, these environments are also being progressively degraded by the spread of invasive plant species, such as blackberry (*Rubus ulmifolius* Schott) and Australian blackwood (*Acacia melanoxylon* R. Br.), among others, which are rapidly colonizing increasingly larger areas of the hill range (Zaninovich et al., 2023). Due to its varied and effective proliferation strategies, the Australian acacia is an invasive tree particularly challenging to eradicate. This species releases allelopathic compounds that inhibit the growth of neighboring plants; accumulates biomass in the soil, acting as a physical barrier to seedling establishment; and competitively excludes native species through both aboveground and belowground competition for light and other resources. As a result, it frequently establishes near-monocultures, overwhelmingly dominating the landscape. Notably, the root systems of *A. melanoxylon* can access water and nutrients from deeper soil layers than those typically available to grassland species (Le Maitre et al., 2011; Souza-Alonso et al., 2017). This replacement of native flora by acacias is known to cause negative effects on biodiversity, fire regimes, water use, and soil properties. Acacia trees currently exhibit extensive expansion in all mountainous sectors of the Tandilia System (Vieites-Blanco and González-Prieto, 2020).

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In addition to the massive extinction of large mammals since the late Pleistocene (Barnosky and Lindsey, 2010), changes produced by human activity in the last 100 years have led to the extinction of all or a large part of the remaining medium and large mammals of the Pampa´s grasslands ecoregion, such as the jaguar (*Panthera onca*) and the pampas deer (*Ozoteceros bezoarticus*), and have changed the distribution and abundance of many other species (Azpiroz et al., 2012). Among these mammals, carnivores are commonly used as focal species in conservation initiatives (Linnell et al., 2000; Sanderson et al., 2002). This is because they can exert important top-down ecological effects, influencing both community structure and ecosystem function. Predators play a fundamental role in controlling herbivore populations, as well as in controlling their feeding behaviors, indirectly allowing greater plant species abundance due to reduced herbivory pressure (Dirzo et al., 2014; Atkins et al., 2019). These characteristics make them well-suited as biodiversity indicators, guiding conservation actions based on their presence beyond their ecosystem benefits (Natsukawa and Sergio, 2022). Moreover, carnivore species are often used as indicators of an area's conservation status due to the substantial impacts that food limitation and habitat fragmentation can have on their populations (Sergio et al., 2008).

Numerous studies have examined the composition (e.g., (Caruso et al., 2016)) and the trophic characteristics of species within the carnivore assemblages in the Pampas region (e.g., (Canepuccia et al., 2008; Farías and Kittlein, 2008; Guidobono et al., 2016)). However, little is known about how replacing native grasslands with invasive trees, such as blackwood acacias, affects the spatial and temporal composition of carnivore assemblages. The Pampas gray fox (*Lycalopex gymnocercus*) and Geoffroy's cat (*Leopardus geoffroyi*) are two of the most commonly recorded carnivores in the Pampean grassland ecoregion, with the former exhibiting more generalist feeding habits (Manfredi et al., 2004; Canepuccia et al., 2008; Luengos Vidal et al., 2012). These species are primarily crepuscular and nocturnal, making them elusive and difficult to spot (Silva-Rodríguez et al., 2025). In this landscape, native mammals coexist with introduced species with significant potential for ecological disruption, such as the feral pig (*Sus scrofa*), and free-ranging dog (*Canis lupus familiaris*), both of which pose serious threats to native species through predation, competition, or habitat degradation (Herrero et al., 2006; Barrios-García and Ballari, 2012; Zanón-Martínez and Lessa, 2014; Isbell et al., 2023). The feral pig may compete for food (e.g., small prey, carrion, fruits) and habitat with native carnivores (Barrios-García and Ballari, 2012). Furthermore, feral pigs, through their rooting and wallowing behavior, can alter vegetation structure, potentially affecting the availability of shelter for native mammals. These environmental modifications may trigger bottom-up effects in the trophic web, indirectly impacting predators such as Geoffroy's cat and Pampas gray fox (see (Herrero et al., 2006)).

This study aims to describe the assemblage composition of carnivore species in a small protected area of the Tandilia Mountain System (Paititi Private Natural Reserve, PPNR) and to assess the spatial and temporal variation in their activity using camera trapping. To achieve this, we compared areas characterized by native habitats with those invaded by *A. melanoxylon*. Our focus was on the reserve's two most representative and prevalent species: the Pampas gray fox and Geoffroy's cat.

Materials and methods

Study area

This study was conducted in the PPNR (37°55′25″ S, 57°49′12″ W; Fig. 1), which is a member of the Argentine Network of Private Nature Reserves (https://reservasprivadas.org.ar/). The Reserve is located in the southeastern sector of the Tandilia mountain system, Buenos Aires Province, Argentina, and is considered a relic of native grassland. The PPNR features low, isolated hills (Sierra de los Padres) reaching elevations of up to 500 m a.s.l. The landscape includes broad ridges and valleys, with vegetation structured along distinct geomorphic zones: gentle lower slopes dominated by shrubs, grasses, and geophytes; steeper, rocky hillsides with sparse cover; and relatively flat summits characterized by grasslands over loess soils. The climate is temperate, with an average annual rainfall of 850 mm, and summers are often characterized by water deficits, indicating seasonal moisture limitations (Echeverría et al., 2017).

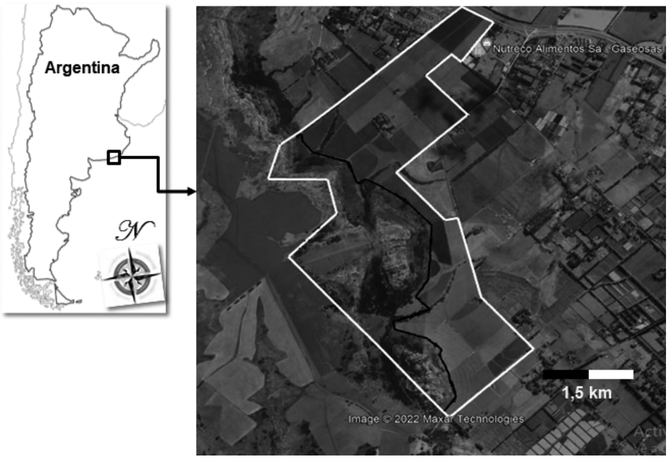

Figure 1 – The Paititi Natural Reserve is located in the Tandilia Mountain System, Buenos Aires Province, Argentina. The area outlined in white represents Estancia Paititi, while the black outline marks the boundaries of the Paititi Private Natural Reserve.

The reserve dedicates 220 hectares to the conservation of the hill range's native habitats (grasslands and shrublands). Due to its high diversity, endemism, and archaeological remains, PPNR has been designated a Valuable Grassland Area (Bilenca and Miñarro, 2004). Additionally, it is recognized as an area of interest for conservation and ecotourism and is part of the Alianza de Pastizal (an alliance between livestock and agricultural producers and conservationists, https://www.avesargentinas.org.ar/alianza-del-pastizal).

The vegetation in the PPNR is characterized by the predominance of *Paspalum quadrifarium* and *P. exaltatum* at the base of the hills, forming a distinctive tall grassland environment (Bilenca and Miñarro, 2004; Arcusa, 2016). On the slopes, shrublands dominated by *Baccharis articulata*, *B. coridifolia*, *B. dracunculifolia*, *Buddleja thyrsoides*, and *Dodonaea viscosa* prevail, alongside characteristic thickets of *Colletia paradoxa*. At the summit, large areas are dominated by ferns of the genera *Rumohra*, *Adiantum*, and *Blechnum*, with rocks covered in mosses and lichens. The invaded area is dominated by *Acacia melanoxylon*, which forms forest stands with a closed canopy, open understory, and a ground layer largely composed of litter (Arcusa, 2016). Across the Tandilia Hill System, this species is a widespread invader (Arcusa, 2016) and currently occupies approximately 18 % of the PPNR (Zaninovich et al., 2023). Acacia patches vary in size and occur interspersed with extensive native grasslands and shrublands. Beyond the foothills, the surrounding plains are dominated by grasslands and agro-pastoral landscapes, whereas the higher elevations of the hills remain less affected by acacia encroachment, supporting a distinctive high-altitude grassland–shrubland ecosystem.

Sampling design

We used camera traps to register the daily activity patterns of mammals in the study area (see (Wearn and Glover-Kapfer, 2019); Appendix 1). Camera traps were active over an average of 15 days in each of the four seasons: winter, spring, summer, and autumn (between June 2022 and May 2023; see Appendix 2). The cameras operated continuously 24 hours a day.

Sixteen camera traps were deployed, with eight cameras placed in each of two distinct environments (i.e., acacia forest vs. grasslands and shrublands). Each camera was set to capture three photos per detection event (in some cases, 10- or 20-second videos were recorded), with a 15-second minimum interval between each event, and utilizing either normal or low PIR sensitivity.

Given the difficulty of individual identification, we minimized pseudoreplication by defining independent detections as those of the same species recorded at the same camera station at least 60 minutes apart. Similar independence thresholds have been widely adopted in camera trap studies on mammals, including those by O'Brien et al. (2003); Di Bitetti et al. (2006), and Wang and Macdonald (2009), who applied intervals of 30 to 60 minutes to define independent capture events. These criteria ensure that each event is more likely to represent a distinct visit or individual, improving data reliability and comparability across studies. Camera traps within the same environmental type were placed at a minimum distance of 100 meters apart. This distance was determined based on the environment patch sizes within the reserve (grassland/scrub or acacia forest), ensuring that both were equally represented. Although the home range of most carnivorous mammals typically exceeds this distance, this spacing is appropriate for assessing relative environmental use and daily activity patterns, in fragmented or heterogeneous landscapes (e.g., (Tobler et al., 2008; O'Brien et al., 2003; Rovero et al., 2013; Sollmann et al., 2013)). Data collection was conducted in two distinct environments: (a) grassland/shrubland and (b) acacia forest, which were defined according to the following criteria:

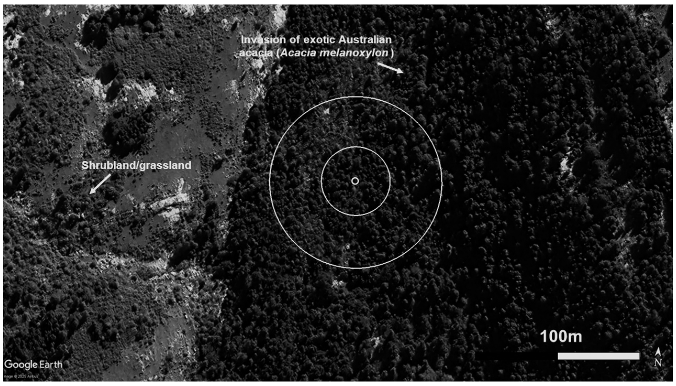

Figure 2 – Example of making circles of 20 ± 0.5 and 50 ± 0.5 meters radius around the point corresponding to a camera trap in Sierra Grande (Paititi Private Natural Reserve) using a Google Earth image. The contrast is also illustrated between an *Acacia melanoxylon*-invaded environment and a natural grassland/shrubland characteristic of the serrano environment. Map scale = 100 m.

Native grassland/shrubland. mixed composition with grassland/shrubland characterized by the predominance of *Baccharis dracunculifolia ssp. tandilensis* and *Paspalum quadrifarium*. These species are distributed from the foothills to the higher elevations.

Acacia forest. areas where the exotic Australian acacia (*A. melanoxylon*) is progressively replacing native grasslands. They have a uniform distribution across various altitudinal zones of the mountain range, from the foothills to the higher elevations of the reserve.

For the placement of the camera traps, locations frequented by wildlife and sites where the vegetation provided some levels of protection were chosen, minimizing contact with livestock or human activity (Online Resource 1). The sites were baited with a minimal dose of canned tuna during the first day of camera trap placement. We manually check all camera records, taking into account the recommendations of Silva-Rodríguez et al. (2025) regarding current quality control practices (see also Apps et al., 2018).

We identified two spatial scales of analysis to investigate the relationship between carnivore presence and activity. The first level of comparison was conducted between the two major environmental units in the reserve: grassland/shrubland (native habitat) vs. Australian acacia forest (exotic habitat). The second level encompassed a broader spatial scale, capturing the environmental heterogeneity resulting from hill topography and the patchy distribution of vegetation. Consequently, an additional variable was quantified to describe the level of landscape heterogeneity at each point corresponding to the location of each camera trap. For this purpose, and to reflect spatial variation in environment composition, two circles of radius 20.0 ± 0.5 m and 50.0 ± 0.5 m were determined (using the camera location as the center) based on the size and distribution of the environments in the reserve (Fig. 2). These distances were selected to capture both the immediate surroundings of the camera and a broader landscape context. The variables considered were the percent coverage of 1) grassland, 2) shrubs, 3) acacia trees, 4) exposed rock, and 5) open areas within the area of the circle, using Google Earth satellite images as a reference. The latter variable refers to zones of short grasses or, in some cases, areas with crops, characterized by having lower vegetation coverage compared to grassland/shrubland areas and acacia woodland. The circle measurements were arbitrarily defined, with the 20 m radius scale intended to capture the vegetation characteristics closest to the camera, while the 50 m radius scale was designed to reflect the broader landscape characteristics of the area surrounding the camera.

Data analyses

Generalized linear mixed models (GLMMs) with a Poisson distribution and an offset (recording hours) were initially fitted to compare the activity patterns of all recorded species. However, due to overdispersion, we used generalized linear mixed models (GLMMs) with a negative binomial distribution, incorporating the same offset and a log link function. The number of photographic capture events of individuals via camera trapping served as the response variable, with species (Pampas gray fox, Geoffroy's cat, skunk, and lesser grison) as the explanatory variable. The location in geographic coordinates of each camera was treated as a random effect, as it was replicated across different seasons. This approach was implemented using the *glmer* function from the lme4 package (Bates et al., 2015). However, after observing that the random variable did not contribute to the variability, it was removed from the model based on a likelihood ratio test comparison with GLMs. Subsequently, generalized linear models (GLMs) with a negative binomial distribution, incorporating an offset (recording hours) and a log link function, were employed using the *glm.nb* function from the MASS package (Venables and Ripley, 2002). Differences among the levels of the fixed factor were assessed through multiple-comparison tests (Tukey Contrasts) using the *multcomp* package (Hothorn et al., 2008).

Given the proximity among camera trap stations, we tested for spatial autocorrelation in the residuals of the GLMs using Moran's I ($p > 0.05$), implemented with the *spdep* package (Pebesma and Bivand, 2023). We used camera trap coordinates to define spatial neighbors within a biologically meaningful threshold based on the estimated home range size of each species (Lucherini and Luengos Vidal, 2008; Manfredi et al., 2012). No significant spatial autocorrelation was detected, indicating that the assumption of independence among stations was met.

To analyze the effect of environmental variables on the activity patterns of the Pampas gray fox and Geoffroy's cat, the same approach was applied. Initially, the correlation between environmental variables was assessed using Spearman's correlation test with the *cor.test* function, excluding variables that showed significant correlation. We considered not only the p-value but also the correlation coefficient (r), ensuring that it remained below 0.5, a threshold commonly used as a general reference in similar analyses. The number of photographic capture events, captured via camera trapping, was used as the response variable, while the explanatory variables included season (autumn, spring, and summer) and environmental percent cover (grassland, shrubs, acacia trees, exposed rock, and open areas) within two predetermined ratios of 20 and 50 meters around each camera trap. This methodology was also repeated to test the daily activity patterns of the Pampas gray fox and Geoffroy's cat, with the response variable remaining as the number of photographic capture events. The explanatory variable, in this case, was the activity period (sunrise, day, sunset, and night), determined based on sunrise and sunset times provided by the Naval Hydrographic Service for the city of Mar del Plata on the sampling start and end dates for each season, which correspond to civil time (also known as civil twilight times; see Appendix 2). All four seasons were included in this analysis. For both the analyses of environmental variables influencing activity patterns and the assessment of daily activity patterns, only the Pampas gray fox and Geoffroy's cat were examined, as these were the only species with a sufficient sample size for meaningful comparisons.

The fitness of all models was checked using DHARMa diagnostic plots employing the DHARMa package (Hartig, 2022). To identify the most parsimonious model, we applied a stepwise backward model selection procedure to eliminate non-significant main effects until only significant terms remained. Model simplification was performed by sequentially comparing nested models using likelihood ratio tests (ANOVA). All tests were two-tailed with a significance level of $\alpha = 0.05$. The results were visualized using the R package visreg (Breheny and Burchett, 2017). Statistical analysis of the data was performed using the R software, Version 4.3.1 (R Core Team, 2023).

Results

Carnivore Assemblage

Four carnivore species present in our records were photographed in both grassland and acacia forests: Pampas gray fox (*Lycalopex gymnocercus*), the Geoffroy's cat (*Leopardus geoffroyi*), skunk (*Conepatus chinga*), and lesser grison (*Galictis cuja*). Numerous native non-target mammal species (e.g., *Oxymycterus rufus*, *Didelphis albiventris*, *Dasypus hybridus*, see details in Online Resource 2) were also recorded. Other non-native species observed in our records, though in low numbers, included hares (*Lepus europaeus*), axis deer (*Axis* axis), wild boar (*Sus scrofa*), rats (*Rattus rattus*), and domestic dogs (*Canis lupus familiaris*).

A total of 582 photographic shots of the Pampas gray fox (251 in grassland/shrubland, 331 in acacia forest), 73 of the Geoffroy's cat (43 in grassland/shrubland, 30 in acacia woodland), 15 of skunks (3 in grassland/shrubland, 12 in acacia woodland), and 14 of lesser grison (11 in grassland/shrubland, 3 in acacia woodland) belonging to the carnivore assemblage were recorded (Fig. 3). Significant differences were observed between species ($X^2 = 121.67$, $p < 0.05$), with the daily records of gray fox being higher than those of the Geoffroy's cat, lesser grison, and skunk ($\beta = 2.0777 \pm 0.2579$, $z = 8.058$, $p < 0.05$; $\beta = 2.8885 \pm 0.3322$, $z = 8.694$, $p < 0.05$; $\beta = 3.8032 \pm 0.3602$, $z = 10.560$, $p < 0.05$). Additionally, the records of the Geoffroy's cat were higher than those of the skunk ($\beta = -1.7255 \pm 0.3764$, $z = -4.584$, $p < 0.05$).

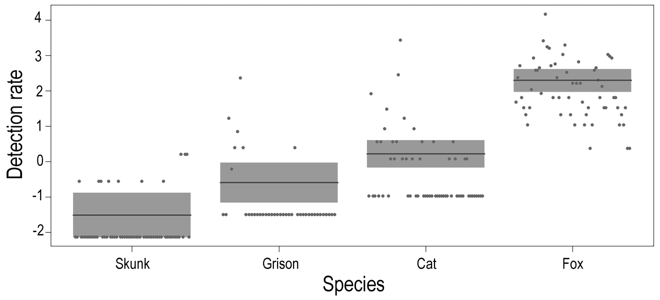

Figure 3 – Partial residuals of the detection rate of the 4 recorded mammal species belonging to the Order Carnivora, considering both environments combined. Plots show a confidence band (shaded area), prediction line (solid line), and partial residuals (points).

Although no statistically significant differences were found in the abundance of lesser grisons relative to skunks or Geoffroy's cats ($\beta = 0.9148 \pm 0.4308$, $z = -2.123$, $p > 0.05$; $\beta = -0.8108 \pm 0.3498$, $z = -2.318$, $p > 0.05$), there were more total records of the Geoffroy's cat compared to grisons or skunks (Fig. 3).

Relationship between Pampas gray fox and Geoffroy's cat with environmental variables

Pampas gray fox

A significant effect on gray fox observation frequency (Tab. 1) was observed at the 20 m radius scale concerning the variables "season", "shrub percentage", and "grass percentage". The occurrence frequency was higher in the spring season ($\beta = 0.836 \pm 0.15$, $z = 5.557$, $p < 0.05$). Moreover, analyses of environmental variables showed a positive relationship between detection rate and shrub cover ($\beta = 0.0077 \pm 0.0019$, $z = 4.137$, $p < 0.05$), while detection frequency decreased as grass cover increased ($\beta = -0.0107 \pm 0.0028$, $z = -3.860$, $p < 0.05$) (Fig. 4A, B; see also Appendix 3).

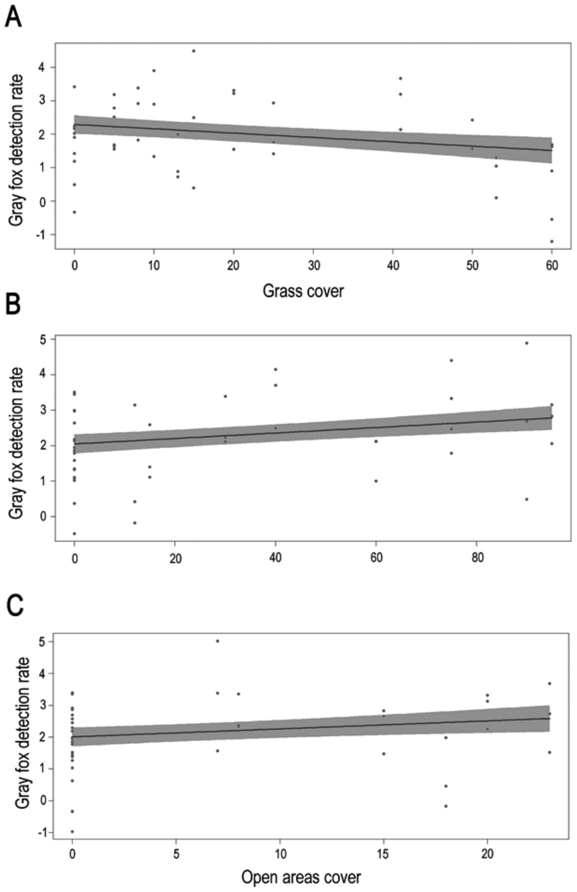

Figure 4 – Panel (A) shows the partial residuals of the Pampas gray fox detection rate concerning shrub abundance with the 20 m radius scale. (B) displays the partial residuals of the Pampas gray fox detection rate concerning grass abundance with the 20 m radius scale. (C) displays the residuals of the Pampas gray fox detection rate concerning the coverage of open areas with a 50 m radius scale. Plots show the model-predicted values (solid line), confidence band (shaded area), and partial residuals (points).

The variables "season" and "open areas" affected the observation frequency of Pampas gray foxes at the 50 m scale (Tab. 1). In this case, a higher detection rate of gray foxes was observed in spring compared to autumn ($\beta = 0.7878 \pm 0.1815$, $z = 4.341$, $p < 0.05$) and summer ($\beta = -0.9286 \pm 0.2206$, $z = -4.210$, $p < 0.05$), as well as a higher detection rate with increased coverage of open areas ($\beta = 0.0252 \pm 0.0096$, $z = 2.621$, $p < 0.05$) (Fig. 4C).

Geoffroy's cat

Considering the area defined by a 20 m radius scale, no variable explained the occurrence frequency of the Geoffroy'cat. The best fit was presented by the null model (Tab. 2). However, at the 50 m scale, higher shrub coverage resulted in more Geoffroy'scat's records ($\beta = 0.029 \pm 0.012$, $z = 2.377$, $p < 0.05$) (Fig. 5A), and there were also more records with lower rock coverage ($\beta = -0.0915 \pm 0.0459$, $z = -1.994$, $p < 0.05$) (Fig. 5B; Tab. 2; see also Appendix 3).

Activity patterns of Gray Fox and Geoffroy's cat

In the combined model, where the frequencies of gray fox and Geoffroy's cat were evaluated within the same model, a higher occurrence frequency of fox ($\beta = 2.0933 \pm 0.1475$, $z = 14.19$, $p < 0.05$; Fig. 6) than of cat was found. Time of day had a significant effect: abundances were higher during the day ($\beta = 1.298 \pm 0.336$, $z = 3.86$, $p < 0.001$)

Table 1 – Results from the stepwise backward model selection procedure for Pampas gray fox data analysis within 20-meter and 50-meter radii.

Response Variable	Explanatory Variable	Final Model		Elimination statistic	
Radius of 20 meters					
Counts		X^2	p-value	X^2	p-value
	Season	29.35	4.2368e-07		
	Schrubs	15.15	9.9555e-05		
	Grass	13.99	0.00018		
Radius of 50 meters					
Counts		X^2	p-value	X^2	p-value
	Season	19.68	5.33e-05		
	Acacia			0.74	0.39
	Exposed rock			0.17	0.68
	Open areas	6.48	0.01		

Table 2 – Results from the stepwise backward model selection procedure for Geoffroy's cat data analysis within 20-meter and 50-meter radii.

Response Variable	Explanatory Variable	Final Model		Elimination statistic	
Radius of 20 meters					
Counts		X^2	p-value	X^2	p-value
	Season			3.38	0.18
	Acacia			1.04	0.31
	Exposed rock			2.00e-4	0.98
Radius of 50 meters					
Counts		X^2	p-value	X^2	p-value
	Season			4.82	0.09
	Schrubs	4.14	0.035		
	Grass			0.196	0.66
	Exposed rock	3.86	0.049		
	Open areas			0.77	0.38

and at night ($\beta = 1.966 \pm 0.328$, $z = 5.99$, $p < 0.001$) compared to sunrise, while sunset did not differ significantly from sunrise ($\beta = 0.301 \pm 0.358$, $z = 0.84$, $p = 0.401$). The effect of environment (grassland vs. reference habitat) was not significant ($\beta = 0.258 \pm 0.224$, $z = 1.15$, $p = 0.249$). No differences between species were observed in the use of native grassland/shrubland environments compared to acacia forests.

No differences were observed in Geoffroy's cat among moments of the day (daily activity). However, a trend towards a higher number of records at sunrise was observed (Fig. 6A). However, differences in daily activity patterns for the Pampas gray fox (Tab. 3) were observed.

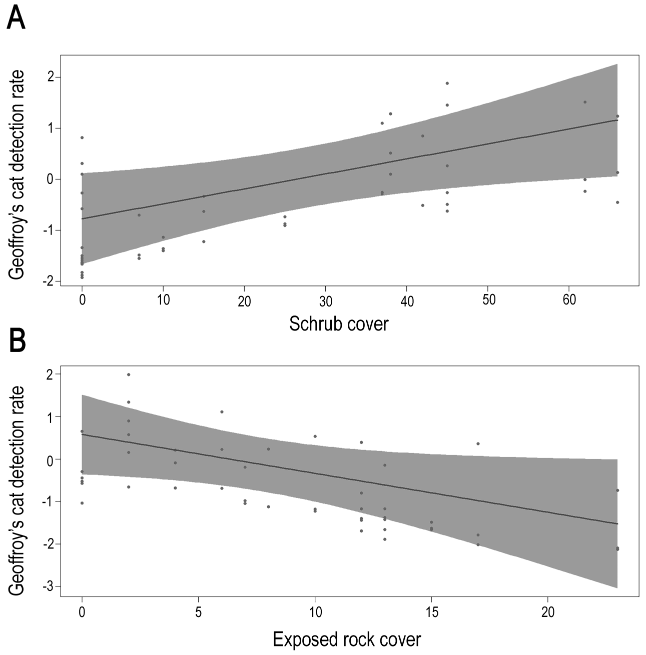

Figure 5 – Partial residual plot showing the detection rate of Geoffroy's cat occurrence concerning shrub abundance (A) and the percentage of exposed rock (B), both with the 50 m radius scale. Plots show the model-predicted values (solid line), confidence band (shaded area), and partial residuals (points).

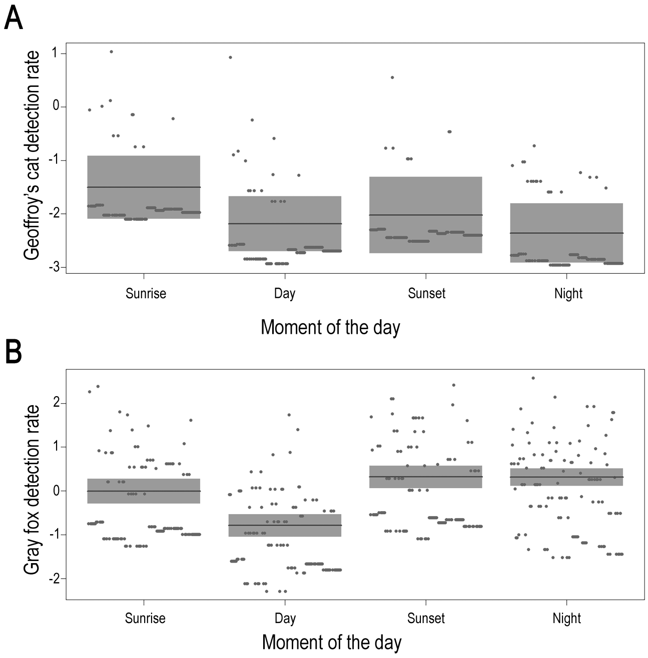

Figure 6 – Boxplot of detection rate of Geoffroy's cat (A) and Pampas gray fox (B) concerning the time of day. For Geoffroy's cat, there were no significant differences between the different times of day, while for the gray fox, fewer records were observed during the day. Plots show the model-predicted values (solid line), confidence band (shaded area), and partial residuals (points).

Table 3 – Results from the stepwise backward model selection procedure for the occurrence frequency of the Pampas gray fox and Geoffroy's cat in the analysis of daily and seasonal activity patterns.

Response Variable	Explanatory Variable	Final Model		Elimination statistic	
Combined model					
Counts		X^2	p-value	X^2	p-value
	Environment	35.61	3.47e-07		
	Species	45.09	1.88e-11		
	Moment of the day	34.87	1.30e-07		
Pampas gray fox					
Counts		X^2	p-value	X^2	p-value
	Environment			0.09	0.75
	Season	49.16	0.04		
	Moment of the day	7.99	1.20E-10		
Geoffroy's cat					
Counts		X^2	p-value	X^2	p-value
	Season	21.17	9.70E-05		
	Environment	5.06	0.02		
	Moment of the day			4.41	0.22

For this species, the day showed fewer observations or records of individuals compared to sunrise ($\beta = -0.7908 \pm 0.1953$, $z = -4.048$, $p < 0.05$), sunset ($\beta = -1.1085 \pm 0.1855$, $z = -5.975$, $p < 0.05$), and night ($\beta = -1.1495 \pm 0.16635$, $z = 6.910$, $p < 0.05$) (Fig. 6B).

Significant differences between seasons were found for the Geoffroy's cat (Tab. 3), with higher record rate in winter than in autumn ($\beta = 1.9496 \pm 0.5700$, $z = 3.420$, $p < 0.05$) and then in summer ($\beta = 2.1504 \pm 0.8236$, $z = 2.611$, $p < 0.05$), and higher in spring than in autumn ($\beta = 1.4866 \pm 0.4672$, $z = 3.182$, $p < 0.05$) (Fig. 7A). No seasonal activity differences were observed for the Pampas gray fox (Fig. 7B; Appendix 3).

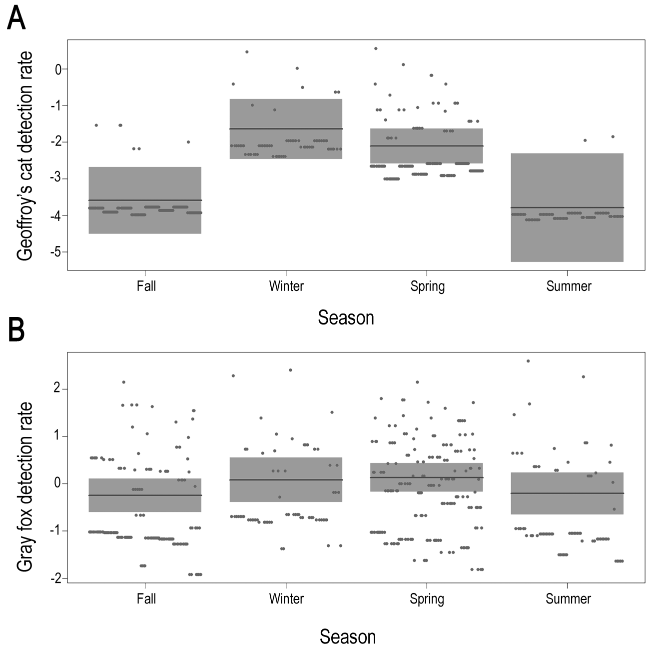

Figure 7 – Partial residuals plot of detection rate of the Pampas gray fox (A) and Geoffroy's cat (B) by seasons. No differences were observed between seasons for the gray fox. For Geoffroy's cat, the highest number of observations was recorded in winter, followed by spring, with fewer observations in autumn and summer. Plots show the model-predicted values (solid line), confidence band (shaded area), and partial residuals (points).

Discussion

During the sampling period, we recorded four of the five native carnivore species known to inhabit the region: Geoffroy's cat, Pampas gray fox, lesser grison (*Galictis cuja*), and skunk (*Conepatus chinga*) (see (Aranguren et al., 2023)). The cougar (*Puma concolor*) was the only carnivore species not observed, despite its confirmed presence in the area, as indicated by occasional sightings reported by residents (E. González Zugasti, pers. comm.). Additionally, we detected the presence of the white-eared opossum (*Didelphis albiventris*) and the southern long-nosed armadillo (*Dasypus hybridus*).

Among the carnivores observed using camera traps, the Geoffroy's cat and the Pampas gray fox had the highest number of recorded sightings. Differences in habitat use and daily activity patterns were observed between the latter species. Contrary to our prediction, no differences were found in habitat use when native grasslands/shrubs were compared with areas invaded by acacia forests. The Pampas gray fox exhibited a higher frequency of occurrence in the studied environments than the Geoffroy's cat. The Pampas gray fox exhibited predominantly crepuscular/nocturnal habits, while Geoffroy's cat did not show a distinct daily activity pattern.

Both species appear to be abundant in the study area. Overall, higher activity levels were recorded for both predators during winter and spring. However, although a trend suggested increased Pampa's fox activity in spring, no statistically significant differences were observed among the four seasons. Seasonal and daily variations in this species may be influenced by climatic factors or fluctuations in agricultural and livestock activities that characterize the region's landscape (Luengos Vidal, 2009). In contrast, comparing the four seasons for Geoffroy's cat revealed more records during winter and spring. This finding diverges from other studies in the Pampas region, which indicate that individuals of this species are primarily active during the summer months (Manfredi et al., 2011).

Habitat use by these species appears to respond to variations in the spatial arrangement of shrub/grassland coverage in the study area (see Online Resource 3). At a finer spatial scale, the presence of the Pampas gray fox was positively correlated with increased shrub coverage at the expense of native grasslands. However, at a larger spatial scale, it was associated with the availability of open areas. In contrast, Geoffroy's cat showed no association with environmental variables at the smallest scale; however, at a larger scale, its occurrence increased with greater shrub coverage and decreased with higher exposed rock coverage.

Most camera trap records in this study corresponded to the Pampas grey fox and Geoffroy's cat, with fewer events documented for smaller predators such as the skunk (*Conepatus chinga*) and the lesser grison (*Galictis cuja*). The low occurrence of these smaller species may be related to spatiotemporal segregation, resulting from their overlap with larger predators, which could negatively affect them (e.g., (Caruso et al., 2016)). Consistent with previous studies, the low number of grison detections in our survey likely reflects the species' inherently low detectability. Camera traps often fail to detect and identify small-bodied species due to limitations related to body size and distance from the camera (Burton et al., 2015). Moreover, their reduced detection frequencies may also be influenced by rapid urbanization, habitat loss, and habitat modification associated with agricultural and livestock expansion, which increase sampling challenges for elusive species despite standardized sampling effort and methodology (Caravaggi et al., 2017). Certain carnivore species, such as *Puma concolor*, either exhibit greater elusiveness to camera trapping or have inherently lower relative abundances. In contrast, other species, such as *Herpailurus yagouaroundi* and *Leopardus colocolo*, are nearly absent from the Pampean region (Luengos Vidal et al., 2019; Pereira et al., 2019; Bisceglia et al., 2019; De Angelo et al., 2019; Castillo and Schiaffini, 2019; Fracassi et al., 2019; Aprile et al., 2019).

The presence of exotic carnivores, such as free-roaming domestic dogs (*Canis lupus familiaris*), also plays a role (Aprile et al., 2019). Dogs without movement restrictions in natural areas are known to significantly affect native carnivore populations globally (Hughes and Macdonald, 2013; Doherty et al., 2017; Mitchell and Banks, 2005), including in protected areas of Argentina (Zamora Nasca and Lambertucci, 2023). Although both the skunk and the lesser grison are generalist species often found in agroecosystems (Castillo et al., 2014; Donadio et al., 2004; Donadio and Buskirk, 2006), they tend to be more abundant in native grasslands farther from human settlements, roads, and other anthropogenic influences (e.g., (Caruso et al., 2016)).

Habitat use by gray fox and Geoffroy's cat

Both the Pampas gray fox and the Geoffroy's cat have a wide distribution range in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. These species are considered relatively common carnivores throughout their distribution area (Pereira et al., 2015; Lucherini, 2016). More generalist carnivores appear to be more tolerant to landscape changes and may even benefit from the development of agricultural and livestock activities (Canepuccia et al., 2008; Caruso et al., 2016; Šálek et al., 2010). They may benefit from and expand their distribution range due to the increased availability and diversity of prey associated with human activities (Macdonald, 1983; Luengos Vidal, 2009; Luengos Vidal et al., 2012).

Particularly, the Pampas gray fox is a generalist South American canid that adapts very well to the human-dominated landscape of the Argentine pampas (Luengos Vidal et al., 2012). This species exhibits considerable ecological flexibility in its diet (Farías and Kittlein, 2008), and daily activity patterns (Luengos Vidal, 2009; Lucherini and Luengos Vidal, 2008; Di Bitetti et al., 2009), and also occupies a wide range of environments in open and transitional areas, including native grasslands and marshes (García and Kittlein, 2005; Canepuccia et al., 2008), and is also commonly found in agricultural and livestock environments within the Pampas region (Lucherini and Luengos Vidal, 2008). Luengos Vidal (2009) recorded that this species selects areas with denser vegetation coverage, either due to more favorable conditions or evasive behavior, such as avoiding human presence. In the Pampas region, patches with greater vegetation coverage throughout the year may serve as a crucial resource for the survival of Pampas gray fox populations. However, both our results and those of Luengos Vidal (2009) agree that vegetation cover is significant at smaller spatial scales, while at larger geographic scales, open environments are more important for the presence of the Pampas gray fox. Although it was expected that this species would primarily utilize native grassland/shrubland environments, as found in other studies (Di Bitetti et al., 2009), the results of this study did not reveal preferences regarding the type of habitat used (grassland/shrubland vs. Australian acacia forests). One possible explanation for this could be the absence of similarly sized competitors, as the Pampas gray fox (4–8 kg) and the Geoffroy's cat (3–5 kg) are among the few carnivores within this weight range in the Tandilia Mountain System, where the puma (*Puma concolor*) is rarely observed. Another possible explanation could be the spatial scale of analysis used in this study. Considering a distance radius of 50 meters from the camera trap, open areas (with short grasses or near crops) largely accounted for the presence of this species. Accordingly, the Pampas gray fox appears to select open landscapes where patches of dense vegetation are nonetheless available as refugia, which would explain the contrasting responses observed at different spatial scales.

Unlike the Pampas gray fox, the Geoffroy's cat exhibits a more specialized diet that is almost exclusively carnivorous, making it less capable of adapting to anthropogenic disturbances and changes in prey abundance (Canepuccia et al., 2008; Caruso et al., 2016). However, like most predators with a wide geographic distribution, its diet varies depending on the environment and the availability of prey, ranging from small rodents to large waterbirds (e.g., (Bisceglia et al., 2008; Canepuccia et al., 2008; Manfredi et al., 2004; Guidobono et al., 2016)). This dietary flexibility may promote a certain degree of ecological plasticity, enabling the Geoffroy's cat to occupy a wide variety of habitats, including scrublands, dry forests, marshes, and grasslands (Manfredi et al., 2006; Canepuccia et al., 2007, 2008; Pereira et al., 2010; Cuyckens et al., 2016). Therefore, this species may also exhibit a certain degree of tolerance to anthropogenic disturbances, allowing it to inhabit agricultural and livestock areas (Cuellar et al., 2006; Castillo et al., 2008).

In this regard, habitat selection by Geoffroy's cat can vary significantly, as studies suggest that this species prefers environments with low levels of anthropogenic disturbance (Manfredi et al., 2006; Cuellar et al., 2006). Conversely, other studies indicate a preference for forest habitats dominated by exotic species over native grasslands or protected areas (Manfredi et al., 2012; Caruso et al., 2016). Our results indicate that vegetation cover is a highly relevant factor concerning space use in this species, likely facilitating prey stalking and providing refuge (e.g., (Canepuccia et al., 2007)). Although this predator also utilizes open areas as movement corridors (Cuellar et al., 2006; Manfredi et al., 2006), an increase in coverage of bare rock coverage may limit opportunities for concealment or shelter. Additionally, forests may provide useful structural features for Geoffroy's cat, given its ability to climb trees, for hunting and shelter ((Manfredi et al., 2006), see Online Resource 4).

As previously noted, this species has a wide latitudinal distribution and exhibits remarkable adaptability to diverse habitats, including grasslands, shrublands, and forests (e.g., (Cuyckens et al., 2016)). Although we initially expected that the lack of understory vegetation in Acacia forests would negatively affect Geoffroy's cat, this environment appears to provide suitable habitat. These findings highlight that species' responses to habitat degradation and to the replacement of native vegetation by exotic species may depend more on their ecological traits than on the native or exotic status of the vegetation.

Although the focal species exhibit a broad home range (with the Pampas gray fox having a home range of 2.13 ± 1.37 km^2, Luengos Vidal 2009, and the Geoffroy's cat ranging between 2.48 and 3.42 km^2, (Manfredi et al., 2012)), the objective of this study was to detect differential habitat use and activity patterns at a small geographical scale. Thus, our study was developed in a relatively small protected area (220 ha) surrounded by an agriculture-dominated landscape matrix. The limitations of working within a relatively small area when studying species with large home ranges are challenges faced by reserve managers; initiatives like ours can provide valuable insights for similar small reserves with patchy habitats. One of the problems of protected areas at a global level is that they are mostly small in size (Schauman et al., 2023). Generating insights into the effects of invasive species on key biodiversity components, such as carnivores, is crucial. Therefore, understanding how sensitive components like carnivores respond to the recurring issue of invasive species presents a fundamental challenge for conservation management in these protected areas. Geoffroy's cat individuals may occupy a specific home range for 4 to 5 months before shifting territories. Therefore, a 12-month sampling period could provide information on different individuals, even though this study covered approximately 6 km in length. Contrary to our original predictions, neither the Pampas gray fox nor the Geoffroy's cat exhibited clear preferences for native grassland or shrubland over Australian acacia forest; rather, both species were observed to traverse and utilize both types of habitats. These species may exhibit considerable ecological flexibility and, consequently, in many cases, they may be less affected by or even benefit from anthropogenic impacts (Luengos Vidal, 2009; Manfredi et al., 2006).

This same impact likely explains why other carnivores, which are more sensitive to habitat changes, have been recorded much less frequently, even when using attractive baits. For instance, the occasional detections of the white-eared opossum (*Didelphis albiventris*) and the southern long-nosed armadillo (*Dasypus hybridus*) may be related to their response to small bait. It is worth noting that the record rate of *D. albiventris* in natural settings tends to be much lower than in human-modified habitats (including urban and suburban areas), so the low detection rates observed here could be expected. Although the study encompassed areas of native grassland and shrubland, these habitats were relatively limited in extent within a highly fragmented landscape. Considering that the home ranges of most Carnivora species cover several kilometers, the proximity of populated areas, agricultural and livestock zones, and roads likely affects the spatial use and detection of all species inhabiting this region.

Daily activity patterns in Pampas gray fox and Geoffroy's cat

Unlike herbivores, the availability of food for carnivores follows a daily activity cycle that is linked to the cycles of their prey. Since capture efficiency varies with prey activity, those carnivores that can synchronize their foraging time with periods when their prey is most vulnerable will achieve greater success at a lower cost than those that forage randomly (Zielinski, 1988). In line with this, if prey species alter their activity patterns, the predators' patterns may also change, which could explain differences in activity patterns observed across studies, seasons, and specific habitats. However, in animals with generalist diets, the ability to exploit prey with diverse activity patterns is expected to confer greater flexibility in their temporal activity. The Pampas fox exhibited a predominantly crepuscular and nocturnal activity pattern, consistent with findings from other studies in the Pampas region (Luengos Vidal, 2009; Lucherini and Luengos Vidal, 2008). However, in natural areas with less human disturbance, this species has been reported to display greater diurnal activity (Luengos Vidal, 2009; see also Di Bitetti et al., 2009). Given its behavioral plasticity, it is likely that in this area, the fox adjusts its daily activity patterns to balance resource acquisition (e.g., aligning with prey activity periods) and risk minimization (e.g., avoiding predation, agonistic interactions with dogs, or disturbances from human activities).

Regarding the Geoffroy's cat, we did not observe a clear preference for specific times of the day. While previous studies suggest it is more active during twilight and nighttime (Castillo et al., 2008; Pereira et al., 2010; Cuellar et al., 2006), this species is also known to adapt its activity patterns in response to periods of lower prey availability, even shifting to hunting diurnal prey (e.g., Pereira et al., 2006; Pereira, 2010). Another reason that could explain the shift away from nocturnal habits in this species may be the energetic demands of maintaining body temperature during the night in environments where temperatures significantly decrease. Thus, a reduction in nocturnal activity could also be attributed to increased energy conservation, competition, or the avoidance of predation (Zielinski, 1988).

This daily pattern may also be linked to differences in habitat preferences and environmental segregation between the larger predators. The Pampas gray fox, which is associated with more open areas, tends to move during low-light hours to reduce its detectability. In contrast, the Geoffroy's cat, which is more commonly associated with dense foliage, is less likely to be detected, suggesting that its activity patterns may not be strongly influenced by light levels.

Future studies should aim to incorporate seasonal variation and climatic factors in order to more comprehensively assess their effects on mammals' activity patterns and habitat use, particularly considering how energetic and reproductive trade-offs may modulate these behavioral responses.

Final considerations

Protected areas are designated geographic spaces aimed at long-term nature conservation, representing a crucial strategy to mitigate the expansion and impact of human-induced stressors on biodiversity and ecosystem services (IUCN, 1994). Globally, these areas face two main challenges: insufficient coverage across various biomes, small size and fragmentation of habitats complicating conservation efforts (Schauman et al., 2023). In such a context, this study provides the first insights into the activity patterns and habitat use of two representative carnivore species in the mountainous environments of the Pampas, impacted by the colonization of exotic *A. melanoxylon*, and the fragmentation of the native grasslands. The high frequency of mesocarnivores in the PPNR, particularly near agricultural fields and areas with regular human activity (e.g., agricultural workers, tourists, and sporadic poachers) highlights the importance of this Reserve in providing habitat for these native species. Frequent daytime recordings of these carnivores in camera traps suggest that the individuals are familiar with their surroundings. If human activity were perceived as a threat, increased nocturnal activity would likely be observed (e.g., see also (Luengos Vidal, 2009; Pereira, 2010)). Additionally, no preference was found for native grassland/shrubland environments over monospecific Australian acacia forests for either species. However, the lack of a clear response to acacia invasion should be approached cautiously, as this invasive species in PPNR is generally distributed in small patches surrounded by grasslands and shrublands. Thus, despite the habitat flexibility of these abundant carnivores, further evaluation is required to assess their responses to extensive areas dominated by acacia in the absence of grasslands and shrublands. Such assessments will provide a clearer understanding of their potential impacts on native fauna diversity and habitat use.

Author contributions

Conceptualization: F.N.B., J.P.I., A.D.C., and M.S.M.; Sampling design and data acquisition: F.N.B., J.P.I., A.D.C., and M.S.M.; resources: J.P.I., E.G.Z. and M.S.M.; investigation and data analysis: F.N.B., J.P.I., A.D.C., T.O. and M.S.M.; funding acquisition: J.P.I. and M.S.M.; writing original draft: F.N.B., J.P.I. and M.S.M.; writing review and editing: F.N.B., J.P.I., A.D.C., T.O. and M.S.M.

Conflict of Interest Statement

The authors have no conflict of interest to declare.

Consent for publication

All authors consent to the publication of this manuscript.

Statement of Animal Ethics

Not applicable to this study.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Appendix 1 Locations of cameras.

Appendix 2 Table showing the sunrise and sunset times for Mar del Plata, provided by the National Service of Naval Hydrography.

Appendix 3 Table S1: Results of models testing the effects of season and vegetation cover on the number of counts for Pampas gray fox data analysis within 20-meter and 50-meter radii.

Appendix 3 Table S2: Results of the Tukey pairwise comparisons among seasons for Pampas gray fox data analysis within 20-meter and 50-meter radii.

Appendix 3 Table S3: Results for models testing the effects of season and vegetation cover on the number of counts for Geoffroy's cat data analysis within 20-meter and 50-meter radii.

Appendix 3 Table S4: Results of the combined model testing the effects of species, moment of the day, and environment on counts.

Appendix 3 Table S5: Results of the Tukey pairwise comparisons among moment of the day for the combined model.

Appendix 3 Table S6: Results of the models testing the effects of season and moment of the day for Pampas gray fox data.

Appendix 3 Table S7: Results of the Tukey pairwise comparisons among times of day for Pampas gray fox data.

Appendix 3 Table S8: Results of the models testing the effects of season and time of day for Geoffroy's cat data.

Appendix 3 Table S9: Results of the Tukey pairwise comparisons among seasons for Geoffroy's cat data.

Supplementary Material 1 Location of 16 camera traps deployed in spring, summer, and autumn in the hilly sector of the Paititi Private Nature Reserve.

Supplementary Material 2 Table containing all species of mammals registered by camera trapping.

Supplementary Material 3 Photos of the selected camera trap sites are displayed, showcasing shrubland/grassland in the two top pictures and acacia forest environments in the two bottom pictures.

Supplementary Material 4 Image taken by a camera trap showing a Geoffroy's cat climbing an Australian acacia tree.