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ABSTRACT

Monitoring the invasive exotic species and their effect on the native fauna is fundamental for effective control. The exotic mammals *Axis axis* and *Sus scrofa,* were introduced in the Argentine territory approximately in 1928 and 1906 inhabiting, at present, four and fifteen protected natural areas, respectively. The objective of this work is to evaluate the distribution and spatio-temporal overlap of native and exotic, medium- and large-sized fauna in a national park of Central Argentina, in order to consider potential negative interactions between them. Camera-traps were distributed in 27 sites between 2017 and 2019 in El Palmar National Park, Argentina. Spatial and temporal overlap was estimated for every pair of exotic-natie taxa. With 2673 camera-days, two exotic: *Axis axis* and *Sus scrofa* and seven native taxa: *Hydrochoerus hydrochaeris*, *Rhea americana*, armadillos, foxes, *Subulo gouazoubira*, *Leopardus geoffroyi* and *Nothura maculosa* were detected. This research could affirm that exotic species are widely distributed in the National Park, but would not restrict the distribution of native species, having the possibility of interacting and, perhaps disturbing, the use of the area. In turn, there was a low overlap in the temporal activity of the exotic and native species when they share the food resources, but a high overlap with most of the other native species, although they differ in their peaks of maximum activity. The existence of variations found in the activity patterns with respect to other areas where the species inhabit could be showing a segregation in the daily activity to avoid the competition.

SHORT ABSTRACT

1) This research detects a spatial overlap between exotic mammals and native fauna that inhabit the El Palmar National Park.

2) The exotic mammals overlapped their activity patterns with the majority of the native fauna, although they differ in their peaks of maximum activity.

3) The existence of variations found in the activity patterns with respect to other areas where the species inhabit, could be showing a segregation in the daily activity to avoid the competition.

KEYWORDS: activity pattern, *Axis axis*, niche, *Sus scrofa*, temporal segregation.

INTRODUCTION

In order to conserve biodiversity, it is necessary to avoid processes that threaten its persistence, such as habitat loss and fragmentation, illegal hunting and species trafficking, forest fires or the presence of invasive exotic species (Margules & Pressey 2000). Particularly, the last one represents a problem in many national parks (Dayer *et al.* 2020; Merino *et al.* 2009), and therefore it is necessary to generate adequate management measures. The control of invasive species implies, first of all, preventing the entry of exotic species, and if they do enter, containing their expansion. On the assumption that they already have an established population, it is necessary to mitigate the damage that the introduced species may cause (Simberloff *et al.* 2013). Studying the biology of the problematic species and monitoring their populations in time and space is fundamental for effective control (Sanguinetti & Pastore 2016).

In general terms, biological invasions were favored by anthropic activity and many of those species were brought in to be used as livestock, pets, commensals or for sport hunting (Long 2003). Exotic species can modify the structure and functioning of invaded ecosystems, altering nutrient cycles and fires (Lovell & Stone 2006), and therefore negatively affecting many native species (Williamson 1996). Biological invasions have been perceived as analogous to natural disasters and are considered one of the most important causes in global loss or change of biodiversity (Ricciardi *et al.* 2011; Sala *et al.* 2000; Wilcove *et al.* 1998). The impacts of biological invasion on a new region depends on both the identity of the invader (intrinsic factors, e.g. body size, locomotion, reproductive rate, population size) and the identity of the host community and ecosystem (extrinsic factors, e.g. transport vectors, local dispersal filters; Valéry *et al.* 2008). When an exotic species coexists with native species with whom shares resources or some dimension of their ecological niches, it can generate new interspecific competition interactions (Mooney & Cleland 2001). These new interactions can be evidenced by a reduction of native species richness and abundance (Blackburn *et al.* 2004; Gaertner *et al.* 2009) but also through morphological differentiations, variations in distribution (Cruz *et al.* 2018) or behavioral changes (Di Bitetti *et al.* 2009).

Globally, the list of species introduced by humans is growing, and so is the number of species that become invasive and have a significant ecological, economic and cultural effect (Mooney & Hobbs 2000). In the absence of specific regulations, these introductions caused widespread damage due to the expansion of several species, in some cases uncontrollable (e.g. Barrios-García and Ballari 2012; Bonino *et al.* 1997; Fasola and Valenzuela 2014; Flueck 2014; Guichón and Doncaster 2008; Merino *et al.* 2009). As in the rest of the world, biological invasions are a serious threat to ecosystems and their biodiversity in South America (Vilà *et al.* 2011), where at least 41% of the most invasive species in the world are already established (Ballari *et al.* 2016; Speziale *et al.* 2012). Currently, there are 23 species of invasive exotic mammals in Argentina (Valenzuela *et al.* 2023), which represents 61% of introduced ones (Merino *et al.* 2009), values far from those expected by the Rule of 10 (Williamson & Fitter 1996), which postulates that one out of ten exotic species achieves establishment and one out of ten established species become invasive (although these values are around 5%, Williamson 1999).

The exotic mammals *Axis axis* and *Sus scrofa*, were introduced in Argentine territory in the beginning of the 19 century from India and Eurasia and northern Africa, respectively (Duckworth *et al.* 2015, Long 2003). Currently, they inhabit four and fifteen protected natural areas from Argentina, respectively (Valenzuela *et al.* 2023). Specifically, in El Palmar National Park these species were introduced in 1970 (*S. scrofa*) and 1980 (*A. axis*) for hunting and commercial purposes (Crespo 1982; Gürtler *et al.* 2017), not applying the first measure to control the invasion of exotic species proposed by Simberloff *et al.* (2013). In view of this fact, the National Park began hunting control management in 2006 (second measure to control invasion), partially successful for *S. scrofa* (decreased its abundance) but not for *A. axis* (Gürtler *et al.* 2017, 2018). So, in this research, the populations of the problematic species were monitored to try to mitigate the potential damage.

Based on the above, the general objective of this work is to evaluate the distribution and spatio-temporal overlap of native and exotic, medium- and large-sized fauna in a national park of central Argentina, in order to consider potential negative interactions between them. In this work, it was determined that the native and exotic species have the possibility of interacting and disturbing each other if they have similar daily activity patterns and spatial distribution.

MATERIALS AND METHODS

Study area

This research was conducted in El Palmar National Park (8500 ha., EPNP), located in Entre Ríos province, in central Argentina (between 31°49'S - 31°55'S and 58°11'W - 58°18'W, Figure 1). It belongs to the Pampa eco-region (Bilenca *et al.* 2004; Brown & Pacheco 2005) and it was created in 1965 by the argentinean national law No. 16802 with the objective of conserving the *Butia yatay* palm tree savannas. The climate is temperate-humid, with an average annual temperature of 17.9 °C that can vary between 24.8 °C in January and 11.7 °C in June. The average annual precipitation value is 1200 mm (APN Management Plan 2015). The most common vegetation communities consist of dense palms groves, shrublands with tall and sparse palm trees, shrublands with young palm trees, grasslands with tall sparse palm trees, and open grasslands with tall graminoids (Batista *et al.* 2014).

Camera trapping surveys

Camera-traps (Bushnell, with infrared flash) were distributed in 27 sites from April 2017 to March 2019 (Figure 1). Each site was sampled between one and five times (totaling seven study times) along that period, and the cameras were active between 16 and 95 days per time. The camera traps were located at 60 centimeters from the ground and took two photos per detection, with a delay of one second. All photos were taken with a 5MP resolution. The minimum and maximum distances between cameras installed at the same time was 372 and 9303 meters, respectively.

Data analysis

The species or taxon (when species were not possible to differentiate) and the number of individuals were identified by visual inspection on a photo-by-photo basis. Photos were labeled and sorted according to species (or taxon), season (autumn, winter and spring-summer) and period of the day using digiKam 7.2.0 (digiKam Development Team 2021) and R package *camtrapR* (Niedballa *et al.* 2016). For all analyses, the presence of a taxon at a given site and time was defined as the record of the taxon in a photo, regardless of the number of individuals. Two records of the same species were considered independent if the difference between photos was of over 60 minutes (Di Bitetti *et al.* 2014; Gracanin & Mikac 2022). Three periods of the day were defined: day, night and twilight. Twilight includes the period from one hour before and after the average sunrise and sunset time in each season of the year, which were collected from the Sunrise Maplog: https://sunrise.maplogs.com.

Spatial overlap between native and exotic taxa recorded (using the numbers of records of each species per site) was assessed by means of the Morisita-Horn index (or simplified Morisita index, Horn 1966) for each season of the year with the package *spaa* (Zhang 2016). This index takes into account the relative abundance of each species in each site and goes from 0, when the distribution is completely distinct, to 1, when both species have identical spatial distribution (Horn 1966).

A chi-square (χ^2) test was performed to evaluate if the number of records in the day, night and twilight are adjusted to the proportion of hours included in each period. This analysis did not include categories for which the expected frequency was less than 5. Additionally, the selectivity for the period i (w_i) was calculated for each species following Manly *et al.* (2002) as: $w_i = o_i / \pi_i$ where o_i is the proportion of independent records in period i, and π_i is the total hours of the period i/24 hs. The time period is selected when $w_i > 1$ and the time period is avoided when $w_i < 1$ (Bu *et al.* 2016; Gerber *et al.* 2012; Ogurtsov *et al.* 2018). The species were classified according to their habits (time period selected) as nocturnal, diurnal or crepuscular. In the cases where no time period was selected (χ^2 less than 0.10), the species was defined as cathemeral.

To determine whether the activity patterns of the different species varied among seasons, the Mardia-Watson-Wheeler homogeneity test (MWW, Batschelet 198; Mardia 1972; Mendoza Sagrera 2020) was performed with the package *circular* (Lund *et al.* 2022) for species with, at least, 10 records per season. Overlap in activity patterns between each of the exotic species with the rest of the native taxa was assessed by means of the overlap coefficient (Δ, Schmid & Schmidt 2006). This coefficient is a quantitative measure ranging from 0 (no overlap) to 1 (identical activity patterns), considering low overlap when $\Delta < 0.50$, intermediate when $0.50 < \Delta < 0.75$ and high overlap when $\Delta > 0.75$. The coefficient Δ_1 was used when the smallest sample size was less than 50 observations, and Δ_4 was used when the smallest sample size was greater than or equal to 50 observations (Meredith & Ridout 2021). To detect whether the activity patterns between each pair of species differed significantly from each other, the Mardia-Watson-Wheeler homogeneity test was used for species with, at least, 10 records per season (Batschelet 1981). All statistical analyses were performed with

RStudio 2022.07.02 (RStudio Team 2022) and R version 4.2.2 (R Core Team 2022). Finally, for descriptive purposes only, the night period was divided into three thirds: early night, middle night and late night.

RESULTS

With a total sampling effort of 2673 camera-days (687 in autumn, 905 in winter, and 1081 in spring-summer), 33064 photos of two exotic and seven native taxa were taken, with 2829 of them (8.6%) being independent records. *Axis axis* (Erxleben, 1777) (Artiodactyla, Cervidae, exotic) was recorded in 44.3%, *Hydrochoerus hydrochaeris* (Linnaeus, 1766) (Rodentia, Caviidae, native) in 35.0%, *Rhea americana* (Linnaeus, 1758) (Struthioniformes, Rheidae, native) in 5.2%, armadillos (order Cingulata, native) in 4.9%, foxes (family Canidae, native) in 4.4%, *Sus scrofa* Linnaeus, 1758 (Artiodactyla, Suidae, exotic) in 3.0%, *Subulo gouazoubira* (G. Fischer, 1814) (synonym of *Mazama gouazoubira,* Bernegossi *et al.* 2022, Artiodactyla, Cervidae, native) in 1.7%, *Leopardus geoffroyi* (d'Orbigny & Gervais, 1844) (Carnivora, Felidae, native) in 1.5% and *Nothura maculosa* (Temminck, 1815) (Tinamiformes, Tinamidae, native) in 0,04% of the independent records. The records of *A. axis* included between one to six individuals in the same photo, *S. scrofa* one to ten, *H. hydrochaeris* and *R. americana* one to five, foxes one or two and, armadillos, *S. gouazoubira* and *L. geoffroyi* only one. Additionally, camera traps recorded offspring of *A. axis*, *S. scrofa*, *H. hydrochaeris* and *R. americana.* All species are categorized both globally and nationally as Least Concern, except the *R. americana* which is considered globally as Near Threatened (BirdLife International 2022) and nationally as Vulnerable (Rabuffetti & Cerezo 2017).

Spatial distribution

Considering the total data set of the study, *A. axis* was present in 96.3% (all sites except one), *H. hydrochaeris* in 66.7%, Canidae in 51.9%, Cingulata and *S. gouazoubira* in 44.4%, *R. americana* in 37.0%, *S. scrofa* in 33.3% and *L. geoffroyi* was recorded in 25.9% of the 27 sites (Figure 2 A-H), with some differences in the proportion of the occupied sites among seasons of the year for the same species (Table 1).

In general terms, the spatial overlap between native and exotic species was higher in winter (Morisita-Horn index > 0.50), than in autumn and spring-summer (Morisita-Horn index < 0.30). *Axis axis* presented the highest values of spatial overlap with *H.*

hydrochaeris along all seasons of the year, and with *L. geoffroyi*, Cingulata and Canidae in winter. *Sus scrofa* had greater overlap particularly with Cingulata in winter (Table 2). The spatial overlap between both exotic species was low and did not vary between seasons (Table 2).

Temporal distribution

All species selected one or two periods of the day to be active (none cathemeral habit, Table 3, Figure 3 A-H). *Rhea americana* was diurnal in all seasons and did not vary its activity patterns among seasons ($MWW_{\text{among seasons}} = 1.24$, $p = 0.872$, Table 3, Figure 3C). *Subulo gouazoubira* presented diurnal habit in autumn and winter, and crepuscular habit in winter and spring-summer ($MWW_{\text{between autumn and spring-summer}} = 4.11$, $p = 0.12$, Table 3, Figure 3G). *Hydrochoerus hydrochaeris* was principally crepuscular, with crepuscular/nocturnal habits in spring-summer ($MWW_{\text{among seasons}} = 88.03$, $p < 0.001$, Table 3, Figure 3B). The rest of the native species and the exotic ones were crepuscular/nocturnal (Table 3). The armadillo ($MWW_{\text{among seasons}} = 8.02$, $p = 0.091$, Figure 3D), foxes ($MWW_{\text{among seasons}} = 7.76$, $p = 0.101$, Figure 3E) and *L. geoffroyi* ($MWW_{\text{between autumn and winter}} = 7.76$, $p = 0.101$, Figure 3H) did not vary their activity pattern along the season, while *A. axis* ($MWW_{\text{among seasons}} = 38.95$, $p < 0.001$, Figure 3A), *H. hydrochaeris* ($MWW_{\text{among seasons}} = 87.95$, $p < 0.001$, Figure 3B) and *S. scrofa* ($MWW_{\text{among seasons}} = 10.19$, $p = 0.037$, Figure 3F) did.

Both exotic species shared their activity habits with almost all native species of the National Park (Table 3). Particularly, *A. axis* overlapped their activity with all species in all seasons of the year (Table 4), although in less degree with *R. americana* (Δ range: 0.33 - 0.44, Table 4). *Sus scrofa*, the other exotic species, overlapped their activity principally with *H. hydrochaeris*, the foxes and *L. geoffroyi* ($\Delta > 0.5$), but to a lesser degree than *A. axis* in all cases (Table 4).

Although the activity of both exotic species often overlap, the moments with higher frequencies did not strictly coincide (Table 4, Figure 3A & 3F). *Axis axis* showed activity in all the three thirds of the night in autumn and spring-summer while it was more active in early and middle night in winter. On the other hand, *S. scrofa* showed more activity on late-night in autumn and spring-summer, and started in the middle of the night in winter. Differently, armadillos and foxes were always mostly active in the early nights and *L. geoffroyi* had variable daily activities in the different seasons.

DISCUSION

El Palmar National Park (EPNP) is inhabited by both native and exotic faunal taxa of medium and large size, with a greater richness of the first ones, including one species globally categorized as vulnerable (*Rhea americana*, BirdLife International 2022; Rabuffetti and Cerezo 2017). *Axis axis* is considered a species with a moderate level of environmental risk in Argentina (Category B, Lizarralde 2016) and *S. scrofa* is considered a high environmental risk (Category A, Lizarralde 2016), because both generate strong negative impacts on natural environments. One of these impacts is the transmission of viral, bacterial and parasitic diseases, which can be transmitted by direct contact with the species, their feces (brucellosis, tuberculosis, paratuberculosis, toxoplasmosis and leptospirosis), or by their consumption (trichinellosis) (Ballari *et al.* 2019; Marcos *et al.* 2021; Tammone Santos *et al.* 2018). Also, *S. scrofa* can affect the composition and structure of plant and animal communities, promoting the establishment and growth of invasive plants, and also alter soil properties and ecosystem processes (Barrios-García *et al.* 2014; Barrios-García & Ballari 2012; Gürtler *et al.* 2023).

These exotic species had a wide spatial distribution in the EPNP, causing an overlap of their territory with native fauna. However, this overlap was not so high, probably due to the fact that the different taxa occupy the same areas but in different intensity. Also, both exotic species were active principally at night, like most of the native fauna, providing the possibility of temporary encounters in addition to spatial overlap dimension.

According to the principle of competitive exclusion, it is predicted that species with a similar ecological niche cannot coexist indefinitely without exerting strong competition with each other, as this would result in the potential local extinction of one of the species or in the differentiation of some niche dimension (Hardin 1960; Macarthur & Levins 1967). Generally, the three most studied niche dimensions are the spatial, the temporal and the diet. In this research, the first two were analyzed, but it is relevant to take into account the diet of each species in order to understand the possible effect that invasive species may have on native taxa. *Axis axis* is a generalist herbivore (Tellarini *et al.* 2019) that feeds mainly on grasses (Valenzuela *et al.* 2023). In this sense, the diets dimension of the exotic deer would overlap with *H. hydrochaeris, S. gouazoubira* and

R. americana which are folivorous-herbivore (Bolkovic *et al.* 2019; Comparatore & Yagueddú 2016; Juliá *et al.* 2019). In agreement with niche theory (Morris *et al.* 2000), precisely, *A.axis* did not overlap their temporal dimension with two of these tree species. On the other hand, *S. scrofa* is defined as a generalist omnivore by Ballari *et al.* (2019), and as an opportunistic omnivore and mostly herbivore by Valenzuela *et al.* (2023). This type of diet is shared with the two species of foxes cited to the National Park in previous studies *Cerdocyon thous* (Linnaeus, 1766) and *Lycalopex gymnocercus* Fisher, 1814, considered frugivores, scavengers and animalivores, mainly insectivores (Cirignoli *et al.* 2019; Luengos Vidal *et al.* 2019), and with the three species of Cingulata cited previously in the Park *Dasypus hybridus* (Desmarest, 1804), *Dasypus novemcinctus* (Linnaeus, 1758) and *Euphractus sexcinctu*s (Linnaeus, 1758), considered omnivorous and myrmecophagous (Abba *et al.* 2019a, 2019b; Varela *et al.* 2019). Coincident with what was observed for *A. axis*, *S. scrofa* showed a scarce spatial and temporal overlap with the species with similar diet.

At last, in order to know if these spatial and, specially, temporal patterns are typical of the species studied, or if they are the consequence of interference or competition between them, commonly known as ghost of competition (Morris *et al.* 2000), it is necessary to evaluate if these patterns are similar with those detected in other areas of their distribution. As the intensity of competition increases as phylogenetic proximity increases (Di Bitetti *et al.* 2009; Loveridge & Macdonald 2003) and, as aggressive behaviors have been recorded between individuals of the two cervid species present in the EPNP (Cirignoli S., pers. Obs. in Iberá National Park), it is important to analyze the possible competition that exists between these species. It has been suggested that *A. axis* could have the ability to displace other cervids, such as the case of *Blastocerus dichotomus* (Illiger, 1815) in the Paraná Delta (Black-Decima *et al.* 2019). In this work, both cervids overlapped their distribution inside the park at a low level. Additionally, both species did not share the times of day of peak activity. The diurnal habit of *S. gouazoubira* described in EPNP was also described in Ecuador, Brazil, the argentinean Humid Chaco and Peru where was not in sympatry with *A. axis* but with *Mazama americana* (Erxleben, 1777), other possible competing species with nocturnal (Albanesi & Jayat 2016; Ferreguetti *et al.* 2015; Rivero *et al.* 2005) and cathemeral habits (Blake *et al.* 2012; Ferreguetti *et al.* 2015; Huck *et al.* 2017; Tobler *et al.* 2009). However, in other locations of yungas of northwestern Argentina and in the dry tropical forests of Bolivia, where *M. americana also i*nhabit, the habit of *S. gouazoubira* was described as catemeral (Albanesi & Jayat 2016; Juliá *et al.* 2019; Rivero *et al.* 2005). Based on these results, the activity pattern of *S. gouazoubira* could vary according to community composition and, in agreement with the comments of Grotta-Neto *et al.* (2019), could also vary between habitats with different landscapes. It is necessary to take into account that *A. axis*, in its native distribution, is diurnal (Chaudhary *et al.* 2020; Ramesh *et al.* 2015). So, its nocturnal habit recorded in this research may also be a behavioral change due, among other possible causes, to the potential competitors present in the National Park, showing the possibility that both exotic and native species may have the need to vary their behaviors.

Sus scrofa, in its native range (Johann et al. 2020; Keuling et al. 2008), is predominantly nocturnal, which coincides with the results found in this National Park and in forest and crops of Australia and xerophytic deciduous woodlands in Central Argentina (Caley 1997, Caruso et al. 2018). But, in other researches in Argentina and national forest of Rio Grande do Sul, Brazil, this species maintains crepuscular or catemeral habits (e.g. Ballari *et al.* 2019; Silveira de Oliveira *et al.* 2020). The *S. scrofa* activity in EPNP, with a peak activity at approximately midnight, show a possible effect due to the controlled hunting events occurred between 17:00 hs and 23:00 hs (Gürtler *et al.* 2018), generating a possible behavioral change in the species making it more nightly.

In conclusion, this research could affirm that the exotic species of EPNP are widely distributed in the area, but would not restrict the distribution of native species, having the possibility of interacting and, perhaps disturbing, the use of the area. In turn, there was a low overlap in the temporal activity of the exotic and native species when they share the food resources, but a high overlap with most of the other native species, although they differ in their peaks of maximum activity. The variations found in the activity patterns with respect to other areas where the species inhabit, could be showing a segregation in the daily activity to relax the competition (Morris *et al.* 2000). In order to understand if this coexistence between exotic and native species causes not only a change in behavior but also a decrease in the abundance of native species, it would be convenient to continue the study of the community in the long term.

REFERENCES

Abba AM, Superina M, Varela D (2019a). *Euphractus sexcinctus* | Categorización de los mamíferos de Argentina. Available from: http://cma.sarem.org.ar/es/especie-nativa/euphractus-sexcinctus

Abba AM, Torres RM, Superina M (2019b). *Dasypus hybridus* | Categorización de los mamíferos de Argentina. Available from: https://cma.sarem.org.ar/es/especie-nativa/dasypus-hybridus

Albanesi SA, Jayat JP (2016). Patrones de actividad de mamíferos de medio y gran porte en el pedemonte de yungas del noroeste argentino. Mastozoología Neotropical **23**, 335-358.

APN Management Plan (2015). Plan de gestión - Parque Nacional El Palmar (Administración de Parques Nacionales). Available from: https://sib.gob.ar/archivos/Plan_de_Gestion_El_Palmar_Doc_Final.pdf

Ballari SA, Cirignoli S, Winter M *et al.* (2019). *Sus scrofa* | Categorización de los mamíferos de Argentina. Available from: https://cma.sarem.org.ar/es/especie-exotica/sus-scrofa

Ballari SA, Anderson CB, Valenzuela AEJ (2016). Understanding trends in biological invasions by introduced mammals in southern South America: a review of research and management. *Mammal Review* **46**, 229–240. DOI: 10.1111/mam.12065

Barrios-García MN, Ballari SA (2012). Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biological Invasions* **14**, 2283–2300. DOI: 10.1007/s10530-012-0229-6

Barrios-García MN, Classen AT, Simberloff D (2014). Disparate responses of above- and belowground properties to soil disturbance by an invasive mammal. *Ecosphere* **5**, 1–13.

Batista WB, Rolhauser AG, Biganzoli F *et al.* (2014). Las comunidades vegetales de La Sabana del Parque Nacional El Palmar (Argentina). *Darwiniana, nueva serie* **2**, 5–38.

Batschelet E (1981). Circular statistics in biology. *Academic Press, New York*

Bernegossi AM, Borges CH de S, Sandoval EDP *et al.* (2022). Resurrection of the genus *Subulo* Smith, 1827 for the gray brocket deer, with designation of a neotype. *Journal of Mammalogy* **104**, 619–633. DOI: https://doi.org/10.1093/jmammal/gyac068

Bilenca D, Miñarro F, Fischer CG (2004). Identificación de áreas valiosas de pastizal (AVPs) en las pampas y campos de Argentina, Uruguay y sur de Brasil. *Fundación Vida Silvestre Argentina Buenos Aires, Argentina.*

BirdLife International. 2022. *Rhea americana*. *The IUCN Red List of Threatened Species*: e.T22678073A219615764. Available from: https://dx.doi.org/10.2305/IUCN.UK.2022-2.RLTS.T22678073A219615764.en.

Black-Decima P, Camino M, Cirignoli S *et al.* (2019). Tropical Ungulates of Argentina. In: Gallina-Tessaro S, *Ecology and Conservation of Tropical Ungulates in Latin America*. Springer International Publishing: Cham, Switzerland, pp. 291-344. DOI: 10.1007/978-3-030-28868-6_13

Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004). Avian Extinction and Mammalian Introductions on Oceanic Islands. *Science* **305**, 1955–1958. DOI: 10.1126/science.1101617

Blake JG, Mosquera D, Loiselle BA, Swing K, Guerra J, Romo D (2012). Temporal activity patterns of terrestrial mammals in lowland rainforest of eastern Ecuador. *Ecotropica* **18**, 137–146.

Bolkovic ML, Quintana R, Cirignoli S *et al.* (2019). *Hydrochoerus hydrochaeris* | Categorización de los mamíferos de Argentina. Available from: http://cma.sarem.org.ar/es/especie-nativa/hydrochoerus-hydrochaeris

Bonino N, Sbriller A, Manacorda MM, Larosa F (1997). Food partitioning between the mara (*Dolichotis patagonum*) and the introduced hare (*Lepus europaeus*) in the Monte Desert, Argentina. *Studies on Neotropical Fauna and Environment* **32**, 129–134.

Brown AD, Pacheco S (2005). Propuesta de actualización del mapa ecorregional de la Argentina. *La Situación Ambiental Argentina* 28–31.

Bu H, Wang F, McShea WJ, Lu Z, Wang D, Li S (2016). Spatial Co-Occurrence and Activity Patterns of Mesocarnivores in the Temperate Forests of Southwest China. *PLoS ONE* **11**, e0164271. DOI: 10.1371/journal.pone.0164271

Caley P (1997). Movements, activity patterns and habitat use of feral pigs (*Sus scrofa*) in a tropical habitat. *Wildlife Research* **24**, 77–87.

Caruso N, Valenzuela AE, Burdett CL, Luengos Vidal EM, Birochio D, Casanave EB (2018). Summer habitat use and activity patterns of wild boar *Sus scrofa* in rangelands of central Argentina. *PLoS One* **13**, e0206513.

Chaudhary R, Zehra N, Musavi A, Khan JA (2020). Spatio-temporal partitioning and coexistence between leopard (*Panthera pardus fusca*) and Asiatic lion (*Panthera leo persica*) in Gir protected area, Gujarat, India. *PloS one* **15**, e0229045.

Cirignoli S, Pereira JA, Varela D (2019). *Cerdocyon thous* | Categorización de los mamíferos de Argentina. Available from: https://cma.sarem.org.ar/es/especie-nativa/cerdocyon-thous

Comparatore V, Yagueddú C (2016). Diet preference and density of the Greater Rhea (*Rhea americana*) in grasslands of the Flooding Pampa, Argentina. *Revista Brasileira de Ornitologia* **24**, 13–20. DOI: 10.1007/BF03544323

Crespo JA (1982). Introducción a la ecología de los mamíferos del Parque Nacional El Palmar, Entre Ríos. *Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* **15**

Cruz P, Iezzi ME, De Angelo C, Varela D, Di Bitetti MS, Paviolo A (2018). Effects of human impacts on habitat use, activity patterns and ecological relationships among medium and small felids of the Atlantic Forest. *PLoS ONE* **13**, e0200806. DOI: 10.1371/journal.pone.0200806

Dayer AA, Redford KH, Campbell KJ *et al.* (2020). The unaddressed threat of invasive animals in U.S. National Parks. *Biological Invasions* **22**, 177–188. DOI: 10.1007/s10530-019-02128-0

Di Bitetti MS, Di Blanco YE, Pereira JA, Paviolo A, Pírez IJ (2009). Time Partitioning Favors the Coexistence of Sympatric Crab-Eating Foxes (*Cerdocyon thous*) and Pampas Foxes (*Lycalopex gymnocercus*). *Journal of Mammalogy* **90**, 479–490. DOI: 10.1644/08-MAMM-A-113.1

Di Bitetti MS, Paviolo A, De Angelo C (2014). Camera trap photographic rates on roads vs. off roads: location does matter. *Mastozoología Neotropical* **21**, 37-46.

digiKam Development Team (2021). *digiKam*: digiKam API reference page. Available from: https://www.digikam.org/

Duckworth JW, Kumar NS, Anwarul Islam M, Sagar Baral H, Timmins R (2015). *Axis axis*. *The IUCN red list of threatened species*: e.T41783A22158006. Available from: https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T41783A22158006.en

Fasola L, Valenzuela AEJ (2014). Invasive carnivores in Patagonia: defining priorities for their management using the American mink (*Neovison vison*) as a case study. *Ecología Austral* **24**, 173–182.

Ferreguetti ÁC, Tomás WM, Bergallo HG (2015). Density, occupancy, and activity pattern of two sympatric deer (*Mazama*) in the Atlantic Forest, Brazil. *Journal of Mammalogy* **96**, 1245–1254.

Flueck WT (2014). Continuing impacts on red deer from a volcanic eruption in 2011. *European Journal of Wildlife Research* **60**, 699–702.

Gaertner M, Den Breeyen A, Hui C, Richardson DM (2009). Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography: Earth and Environment* **33**, 319–338. DOI: 10.1177/0309133309341607

Gerber BD, Karpanty SM, Randrianantenaina J (2012). Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. *Journal of Mammalogy* **93**, 667–676. DOI: 10.1644/11-MAMM-A-265.1

Gracanin A, Mikac KM (2022). Camera traps reveal overlap and seasonal variation in the diel activity of arboreal and semi-arboreal mammals. *Mammalian Biology* **102**, 341–355. DOI: 10.1007/s42991-021-00218-y

Grotta-Neto F, Peres PHF, Piovezan U, Passos FC, Duarte JMB (2019). Influential factors on gray brocket deer (*Mazama gouazoubira*) activity and movement in the Pantanal, Brazil. *Journal of Mammalogy* **100**, 454–463. DOI: 10.1093/jmammal/gyz056

Guichón ML, Doncaster CP (2008). Invasion dynamics of an introduced squirrel in Argentina. *Ecography* **31**, 211–220.

Gürtler RE, Ballari SA, Maranta AA, Cohen JE (2023). Controlling the abundance of invasive exotic wild boar (*Sus scrofa*) improves palm-tree conservation in north-eastern Argentina. *European Journal of Wildlife Research* **69**, 40. DOI: 10.1007/s10344-023-01668-0

Gürtler RE, Martín Izquierdo V, Gil G, Cavicchia M, Maranta A (2017). Coping with wild boar in a conservation area: impacts of a 10-year management control program in north-eastern Argentina. *Biological Invasions* **19**, 11–24. DOI:

10.1007/s10530-016-1256-5

Gürtler RE, Rodríguez-Planes LI, Gil G, Izquierdo VM, Cavicchia M, Maranta A (2018). Differential long-term impacts of a management control program of axis deer and wild boar in a protected area of north-eastern Argentina. *Biological Invasions* **20**, 1431–1447. DOI: 10.1007/s10530-017-1635-6

Hardin G (1960). The Competitive Exclusion Principle: An idea that took a century to be born has implications in ecology, economics, and genetics. *Science* **131**, 1292–1297. DOI: 10.1126/science.131.3409.1292

Horn HS (1966). Measurement of "Overlap" in Comparative Ecological Studies. *The American Naturalist* **100**, 419-424. DOI: 10.1086/282436

Huck M, Juárez CP, Rotundo MA, Dávalos VM, Fernández-Duque E (2017). Mammals and their activity patterns in a forest area in the Humid Chaco, northern Argentina. *Check List* **13**, 363–378.

Johann F, Handschuh M, Linderoth P, Dormann CF, Arnold J (2020). Adaptation of wild boar (*Sus scrofa*) activity in a human-dominated landscape. *BMC Ecology* **20**, 4. DOI: 10.1186/s12898-019-0271-7

Juliá JP, Varela D, Periago ME *et al.* 2019. *Mazama gouazoubira* | Categorización de los mamíferos de Argentina. Available from: http://cma.sarem.org.ar/es/especie-nativa/mazama-gouazoubira

Keuling O, Stier N, Roth M (2008). How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.? *European Journal of Wildlife Research* **54**, 729–737. DOI: 10.1007/s10344-008-0204-9

Lizarralde M (2016). Especies exóticas invasoras (EEI) en Argentina: categorización de mamíferos invasores y alternativas de manejo. *Mastozoología neotropical* **23**, 267–277.

Long JL (2003). Introduced mammals of the world: their history, distribution and abundance. *Journal of Mammalogy* **85**, 363.

Lovell SJ, Stone SF (2006). The economic impacts of aquatic invasive species: a review of the literature. *Agricultural and resource economics review* **35**, 195–208.

Loveridge AJ, Macdonald DW (2003). Niche separation in sympatric jackals (*Canis mesomelas* and *Canis adustus*). *Journal of Zoology* **259**, 143–153. DOI: 10.1017/S0952836902003114

Luengos Vidal E, Farías A, Valenzuela AEJ, Caruso N (2019). *Lycalopex gymnocercus* | Categorización de los mamíferos de Argentina. Available from: https://cma.sarem.org.ar/es/especie-nativa/lycalopex-gymnocercus

Lund U, Agostinelli C, Arai H *et al.* (2022). R package *circular*: Circular Statistics (version 0.4-95). Available from: https://r-forge.r-project.org/projects/circular/

Macarthur R, Levins R (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist* **101**, 377–385. DOI: 10.1086/282505

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002). *Resource selection by animals: statistical design and analysis for field studies*. 2nd ed. Springer Science & Business Media, Netherlands.

Marcos A, Carpinetti B, Ferro N, Aronowicz T, Dassa L (2021). Percepción del impacto de cerdos cimarrones (jabalíes) sobre la producción agropecuaria de Argentina. *Revista veterinaria* **31**, 131–136.

Mardia KV (1975). Statistics of Directional Data. *Journal of the Royal Statistical Society* **37**, 349–371. DOI: https://doi.org/10.1111/j.2517-6161.1975.tb01550.x

Margules CR, Pressey RL (2000). Systematic conservation planning. *Nature* **405**, 243–253. DOI: 10.1038/35012251

Mendoza Sagrera I (2020). Estadística circular aplicada a la Ecología. *Ecosistemas* **29** DOI: 10.7818/ECOS.1995

Meredith M, Ridout M (2021). *overlap*: Estimates of Coefficient of Overlapping for Animal Activity Patterns. *Central R Archive Network*

Merino ML, Carpinetti BN, Abba AM (2009). Invasive Mammals in the National Parks System of Argentina. *Natural Areas Journal* **29**, 42–49. DOI: 10.3375/043.029.0105

Mooney HA, Cleland EE (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences* **98**, 5446–5451. DOI: 10.1073/pnas.091093398

Mooney HA, Hobbs RJ (2000). Invasive species in a changing world. *Island press*.

Morris DW, Davidson DL, Krebs CJ (2000). Measuring the ghost of competition: Insights from density-dependent habitat selection on the co-existence and dynamics of lemmings. *Evolutionary Ecology Research* **2**, 69–80.

Niedballa J, Sollmann R, Courtiol A, Wilting A (2016). *camtrapR*: an R package for efficient camera trap data management. *Methods in Ecology and Evolution* **7**, 1457–1462. DOI: 10.1111/2041-210X.12600

Ogurtsov SS, Zheltukhin AS, Kotlov IP (2018). Daily activity patterns of large and medium-sized mammals based on camera traps data in the Central Forest Nature Reserve, Valdai Upland, Russia. *Nature Conservation Research* **3**, 68–88.

R Core Team (2022). *R*: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. Available from: http://www.R-project.org/

Rabuffetti FL, Cerezo A (2017). Categorización de las Aves de la Argentina según su Estado de Conservación. *Aves Argentinas*.

Ramesh T, Kalle R, Sankar K, Qureshi Q (2015). Role of body size in activity budgets of mammals in the Western Ghats of India. *Journal of Tropical Ecology* **31**, 315–323. DOI: 10.1017/S0266467415000188

Ricciardi A, Palmer ME, Yan ND (2011). Should biological invasions be managed as natural disasters? *BioScience* **61**, 312–317.

Rivero K, Rumiz DI, Taber AB (2005). Differential habitat use by two sympatric brocket deer species (*Mazama americana* and *M. gouazoubira*) in a seasonal Chiquitano forest of Bolivia. *Mammalia* **69**, 169–183.

RStudio Team (2022). *RStudio*: Integrated Development Environment for R. *RStudio, PBC, Boston, MA*. Available from: http://www.rstudio.com/

Sala OE, Stuart Chapin FIII, Armesto JJ *et al*. 2000. Global Biodiversity Scenarios for the Year 2100. *Science* **287**, 1770–1774. DOI: 10.1126/science.287.5459.1770

Sanguinetti J, Pastore H (2016). Abundancia poblacional y manejo del jabalí (*Sus scrofa*): una revisión global para abordar su gestión en la Argentina. *Mastozoología neotropical* **23**, 305–323.

Schmid F, Schmidt A (2006). Nonparametric estimation of the coefficient of overlapping—theory and empirical application. *Computational statistics & data analysis* **50**, 1583–1596.

Silveira de Oliveira Ê, Ludwig da Fontoura Rodrigues M, Machado Severo M, Gomes dos Santos T, Kasper CB (2020). Who's afraid of the big bad boar? Assessing the effect of wild boar presence on the occurrence and activity patterns of other mammals. *PloS ONE* **15**, e0235312.

Simberloff D, Martin JL, Genovesi P *et al.* (2013). Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* **28**, 58–66. DOI: 10.1016/j.tree.2012.07.013

Speziale KL, Lambertucci SA, Carrete M, Tella JL (2012). Dealing with non-native species: what makes the difference in South America? *Biological Invasions* **14**, 1609–1621.

Tammone Santos A, Condorí WE, Scialfa EA *et al.* (2018). Seroprevalencia de leptospirosis en ciervo axis (*Axis axis*) en el marco del plan de control de mamíferos exóticos invasores del Parque Nacional El Palmar. *II Congreso Internacional de Zoonosis y IX Congreso Argentino de Zoonosis; Ciudad Autónoma de Buenos Aires; Argentina*. 15-15

Tellarini JF, Cirignoli S, Aprile G *et al*. (2019). *Axis axis* | Categorización de los mamíferos de Argentina. Available from: https://cma.sarem.org.ar/es/especie-exotica/axis-axis

Tobler MW, Carrillo-Percastegui SE, Powell G (2009). Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. *Journal of Tropical Ecology* **25**, 261–270.

Valenzuela AE, Anderson CB, Ballari SA, Ojeda RA (2023). Introduced Invasive Mammals of Argentina - SAREM. **3**

Valéry L, Fritz H, Lefeuvre J-C, Simberloff D (2008). In search of a real definition of the biological invasion phenomenon itself. *Biological Invasions* **10**, 1345–1351. DOI: 10.1007/s10530-007-9209-7

Varela D, Abba AM, Superina M (2019). *Dasypus novemcinctus* | Categorización de los mamíferos de Argentina. Available from: http://cma.sarem.org.ar/es/especie-nativa/dasypus-novemcinctus

Vilà M, Espinar JL, Hejda M *et al.* (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology letters* **14**, 702–708.

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998). Quantifying threats to imperiled species in the United States. *BioScience* **48**, 607–615.

Williamson M (1996). *Biological invasions*. Springer Science & Business Media.

Williamson M (1999). Invasions. *Ecography* **22**, 5–12.

Williamson M, Fitter A (1996). The varying success of invaders. *Ecology* **77**, 1661–1666.

Zhang J (2016). *spaa*: SPecies Association Analysis. R package version 0.2.2. Available from: https://CRAN.R-project.org/package=spaa

Table 1: Percentage of sites with presence of each species in each season of the year between April 2017 and March 2019 in the El Palmar National Park, Entre Ríos, Argentina.

Species	Autumn	Winter	Spring - Summer
Axis axis	95	100	100
Hydrochoerus hydrochaeris	63	73	67
Rhea americana	32	40	44
armadillo	47	73	22
foxes	47	80	44
Sus scrofa	32	40	44
Subulo gouazoubira	26	33	44
Leopardus geoffroyi	26	33	22

Table 2: Observed Morisita-Horn index for each pair of exotic-native and exotic-exotic taxon per season of the year in the El Palmar National Park between April 2017 and March 2019, Entre Ríos, Argentina. Values above 0.5 were highlighted in bold.

Taxon 1	Taxon 2	Autumn	Winter	Spring-Summer
Axis axis	*Sus scrofa*	0.38	0.30	0.33
Axis axis	*Hydrochoerus hydrochaeris*	**0.52**	**0.72**	**0.52**
Axis axis	*Rhea americana*	0.09	0.14	0.18
Axis axis	armadillo	0.39	**0.60**	0.28
Axis axis	foxes	0.41	**0.62**	0.28
Axis axis	*Subulo gouazoubira*	0.27	0.37	**0.51**
Axis axis	*Leopardus geoffroyi*	0.18	**0.66**	**0.51**
Sus scrofa	*Hydrochoerus hydrochaeris*	0.28	0.21	0.17
Sus scrofa	*Rhea americana*	0.02	0.11	0.20
Sus scrofa	armadillo	0.42	**0.51**	0.33
Sus scrofa	foxes	0.08	0.14	0.07
Sus scrofa	*Subulo gouazoubira*	0.09	0.48	0.38
Sus scrofa	*Leopardus geoffroyi*	0.12	0.12	0.27

Table 3: Selection index (w) of each temporal category, for taxon and season of the year; χ^2 test to evaluate if the number of records in the day, night and twilight are adjusted to the proportion of hours included in each period in the EPNP between April 2017 and March 2019. wt = $w_{twilight}$; wd = w_{day}; wn = w_{night}. † p-values < 0.10; * p-values < 0.05, ** p-values < 0.01. If any of the expected frequencies of the χ^2 test for each species and season was lower than 5 records, the test could not be performed, and it was marked with - .

Species	Autumn				Winter				Spring - Summer			
	wt	wd	wn	χ^2	wt	wd	wn	χ^2	wt	wd	wn	χ^2
Axis axis	1.63	0.41	1.26	**115.5 ****	1.57	0.42	1.27	**156.4 ****	1.28	0.31	1.60	**167.2 ****
Hydrochoerus hydrochaeris	1.56	0.89	0.88	**24.5 ****	1.74	0.87	0.84	**50.3 ****	1.31	0.39	1.50	**78.9 ****
Rhea americana	0.96	2.22	0.00	-	0.96	2.01	0.18	**22.0 ****	1.17	1.82	0.10	**46.5 ****
armadillo	1.20	0.68	1.19	5.8 †	2.00	0.40	1.13	**27.6 ****	1.26	0.25	1.66	**15.4 ****
foxes	0.67	0.78	1.30	-	1.45	0.28	1.43	**32.9 ****	1.77	0.92	0.77	5.6 .†
Sus scrofa	0.64	0.09	1.88	-	0.67	0.15	1.83	-	1.54	0.55	1.24	5.8 †
Subulo gouazoubira	0.50	1.76	0.55	-	1.33	1.47	0.49	-	1.38	0.73	1.12	-
Leopardus geoffroyi	3.27	0.00	1.00	-	1.80	0.26	1.32	-	1.50	0.00	1.82	-

Table 4: Overlap index (Δ) and Mardia-Watson-Wheeler index (MWW) for each pair of exotic-native and exotic-exotic taxon in El Palmar National Park between April 2017 and March 2019. P-values below 0.05 were marked with *; and p-values below 0.01 were marked with **.

		Autumn		Winter		Spring - Summer	
Taxon 1	Taxon 2	Δ	MWW	Δ	MWW	Δ	MWW
Axis axis	*Sus scrofa*	0.7	**9.1 ***	0.71	**7.6 ***	0.81	1.8
Axis axis	*Hydrochoerus hydrochaeris*	0.79	**37.8 ****	0.79	**49.2 ****	0.84	**10.8 ****
Axis axis	*Rhea americana*	0.44	**42.8 ****	0.33	**60.2 ****	0.34	**107.1 ****
Axis axis	armadillo	0.66	**15.8 ****	0.65	**21.7 ****	0.49	**30.7 ****
Axis axis	foxes	0.85	3.9	0.74	5.3	0.67	**22.6 ****
Axis axis	*Subulo gouazoubira*	0.61	**7.0***	0.58	-	0.76	**6.6 ***
Axis axis	*Leopardus geoffroyi*	0.75	2.2	0.68	2.1	0.59	-
Sus scrofa	*Hydrochoerus hydrochaeris*	0.54	**24.8 ****	0.54	**16.1 ****	0.76	0.4
Sus scrofa	*Rhea americana*	0.27	**27.1 ****	0.1	**28.4 ****	0.5	**32.6 ****
Sus scrofa	armadillo	0.49	6.0	0.68	**13.4 ****	0.49	**21.0 ****
Sus scrofa	foxes	0.64	**7.5 ***	0.66	**7.4 ***	0.79	4.8
Sus scrofa	*Subulo gouazoubira*	0.45	**11.4 ****	0.32	-	0.83	0.8
Sus scrofa	*Leopardus geoffroyi*	0.68	**8.5 ***	0.52	1.7	0.58	-

Figure 1: Location of the studied sites in El Palmar National Park, Entre Rios, Argentina (2017-2019).

Figure 2: Sites where (A) *Axis axis*, (B) *Hydrochoerus hydrochaeris*, (C) *Rhea americana*, (D) armadillos, (E) foxes, (F) *Sus scrofa*, (G) *Subulo gouazoubira*, (H) *Leopardus geoffroyi* were recorded (colored points) at least one time in El Palmar National Park, Entre Ríos, Argentina (2017-2019). White points are sites without records.

Figure 3: Activity patterns of (A) *Axis axis*, (B) *Hydrochoerus hydrochaeris*, (C) *Rhea americana*, (D) armadillos, (E) foxes, (F) *Sus scrofa*, (G) *Subulo gouazoubira*, (H) *Leopardus geoffroyi* for autumn (left panels), winter (center panels) and spring-summer (right panels) in El Palmar National Park, Entre Ríos, Argentina (2017-2019). The n shown represents the number of independent records for each species in each season.

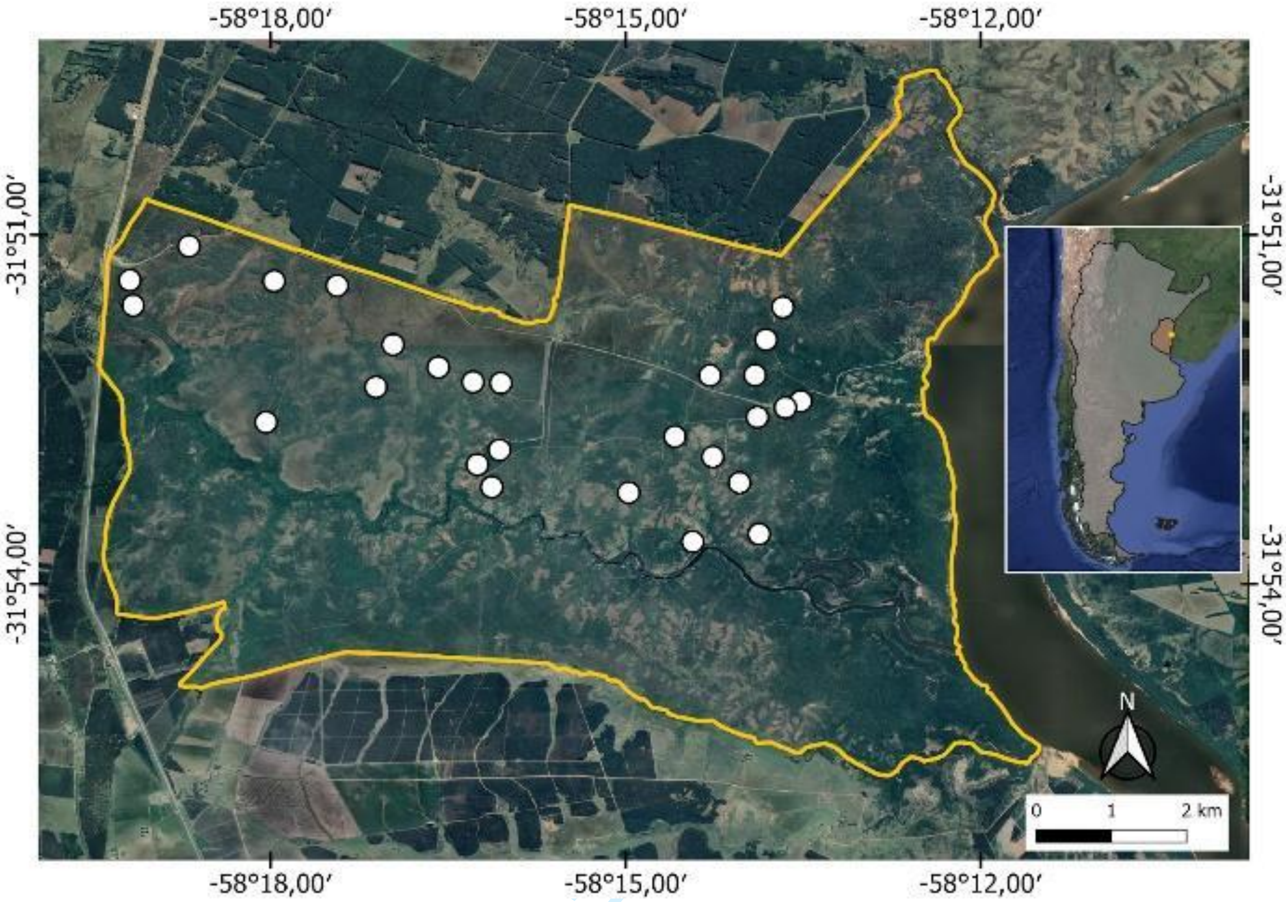


Figure 1.

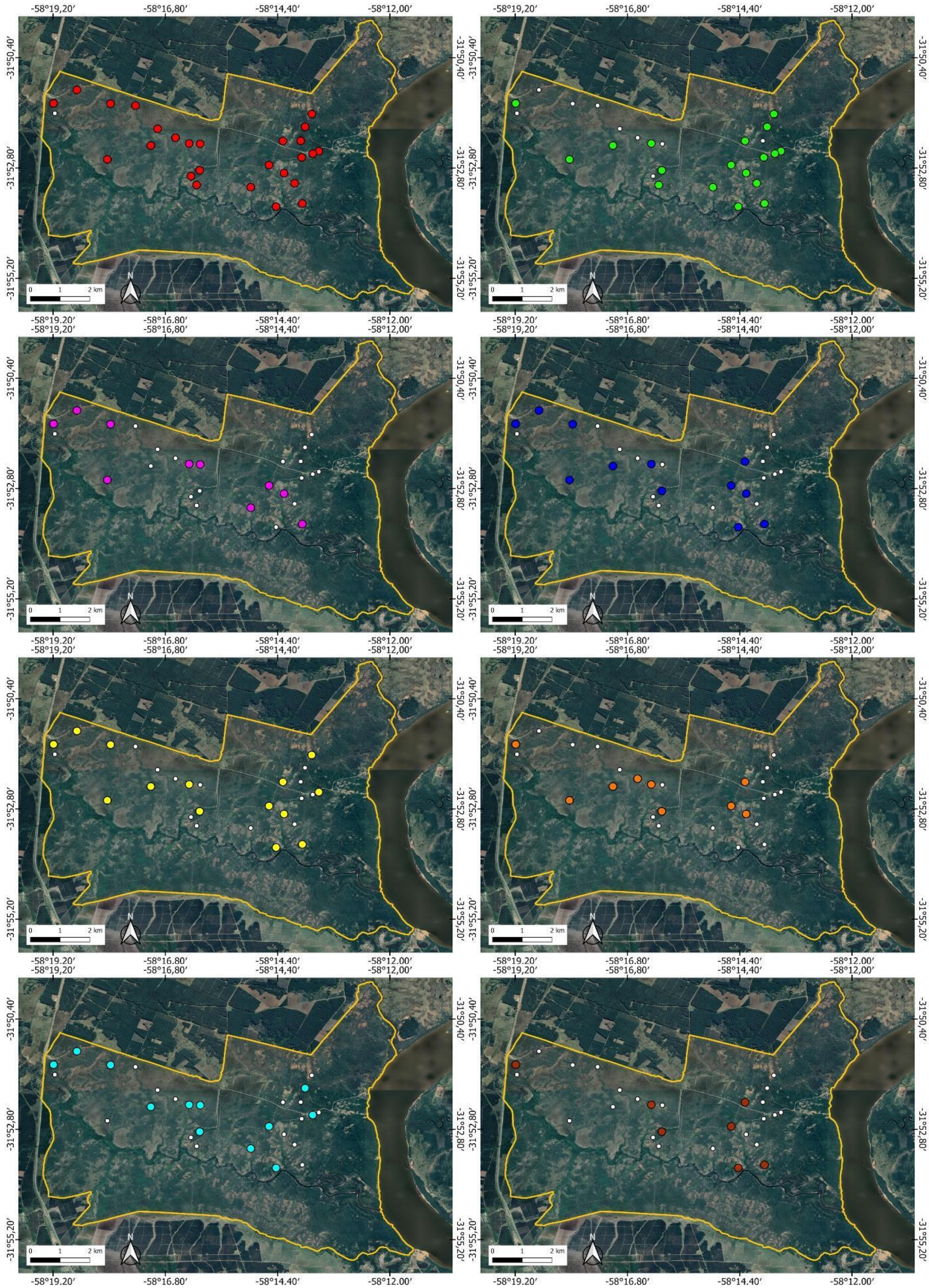
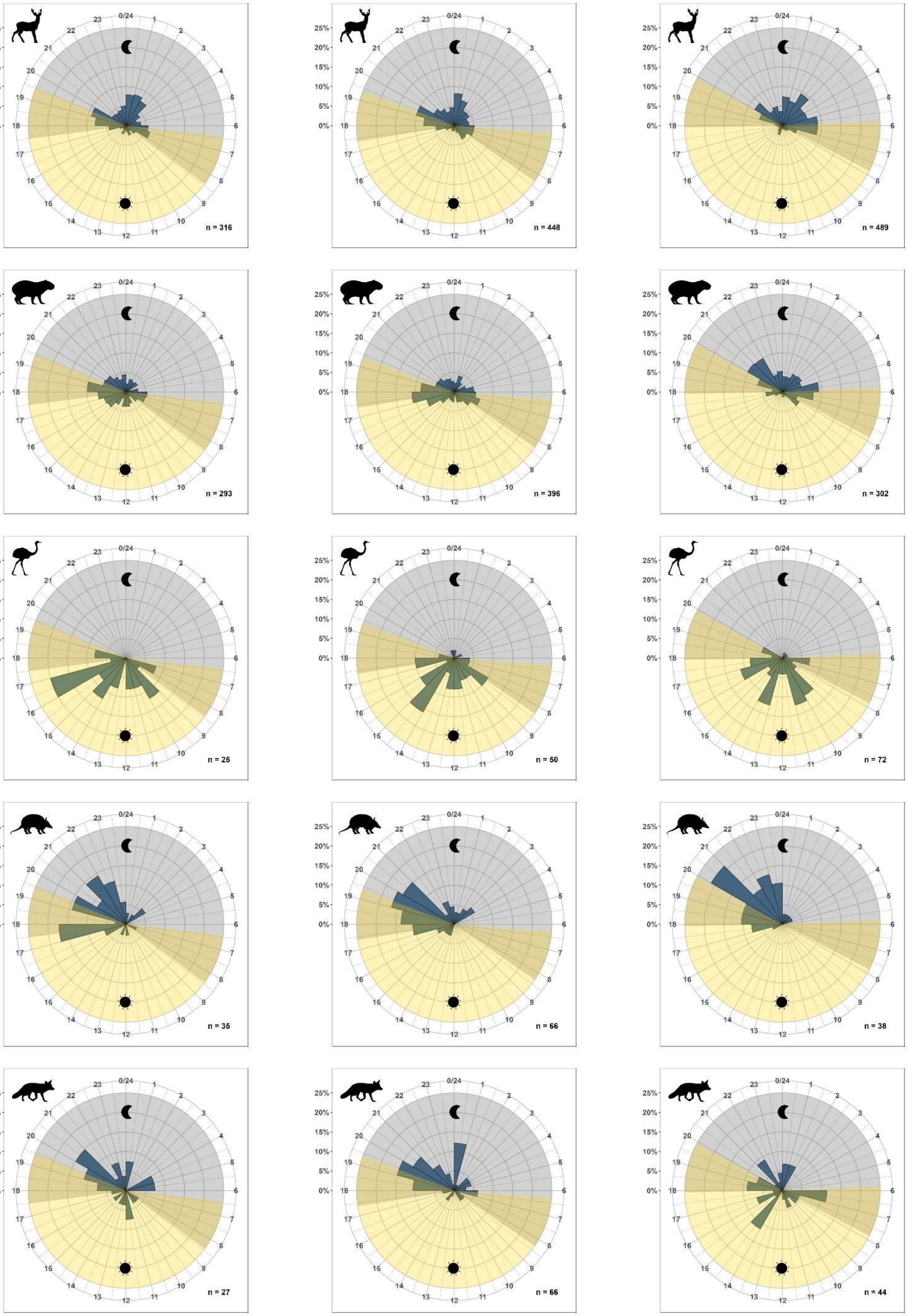


Figure 2 A-H.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n = 66
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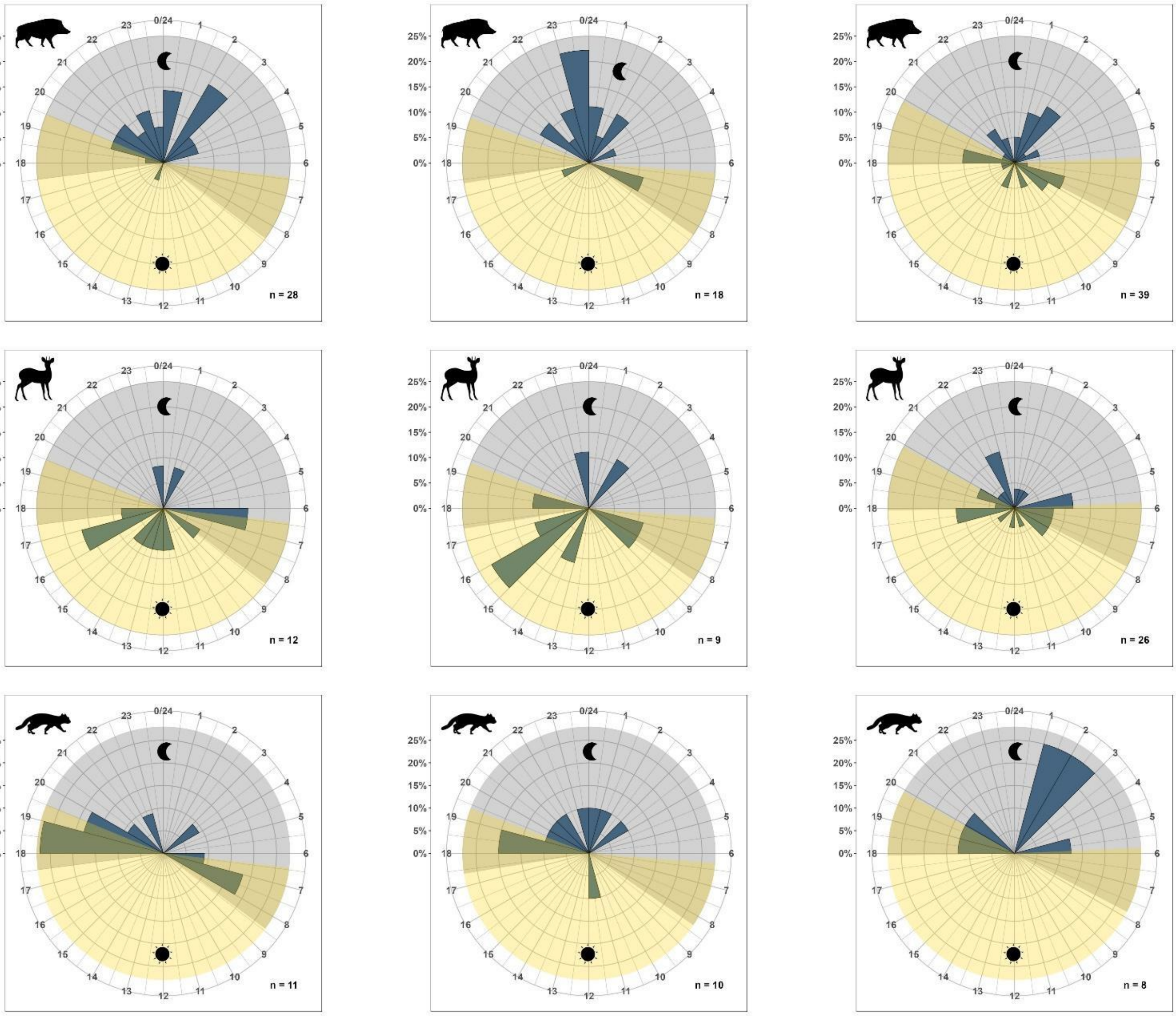
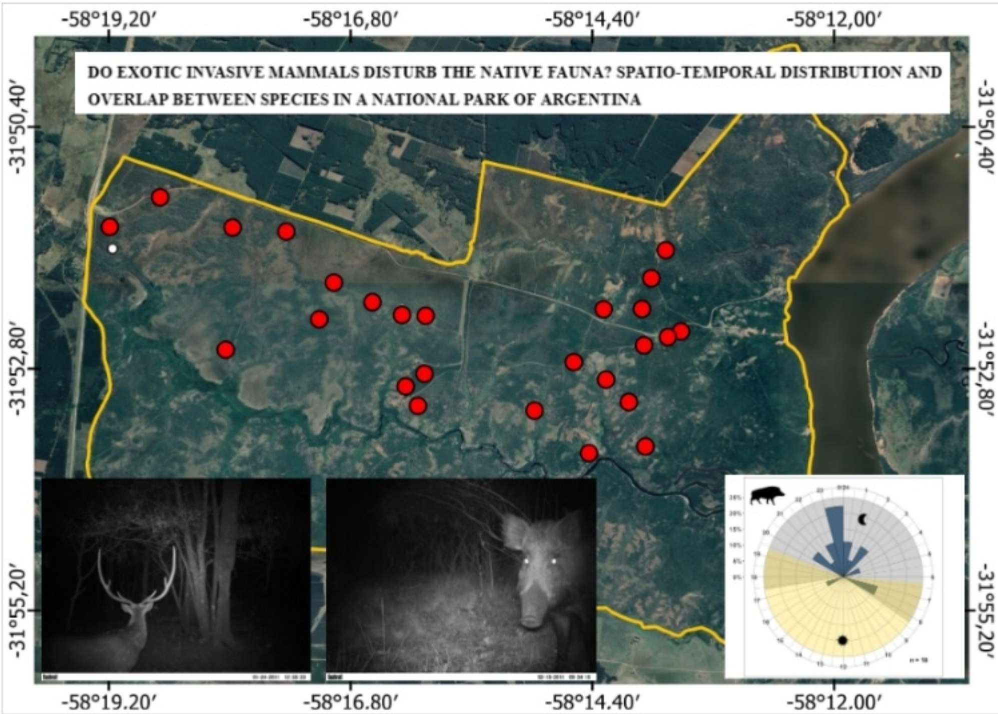


Figure 3 A-H



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