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Habitat use of *Myocastor coypus* in the Ciervo de los Pantanos National Park, Buenos Aires, Argentina

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The present research was carried out in the two main wetlands of the Ciervo de los Pantanos National Park (PNCP), Province of Buenos Aires, Argentina: Laguna Grande (LG) and Juncal del Río Luján (JRL). The objectives were: 1) To corroborate the presence of the coypu, *Myocastor coypus* (Molina, 1782) within the park, so far only confirmed for the coast of the Luján River, and to study the variability between seasons, 2) To evaluate the habitat use of the coypu and the potential variables that determine it through macro and microhabitat scales analysis, and 3) To conduct studies of the spatial disposition of the signs of presence of the species. The last two are fundamental to understanding possible underlying processes, such as food availability or response to the historical hunting pressure. We not only sought to answer which environments of each wetland they use, but also how they use them. The hypotheses were: 1) Sites with signs presence vary between seasons; 2) Sites where signs are present depend on the type of vegetation cover; and 3) Spatial arrangement of signs is clustered. Four transects were surveyed at LG and three at JRL using the transect line method. In each, sites with and without signs were georeferenced, and cover variables of different plant species (%) and water depth (cm) were measured. Generalized linear mixed models (GLMM) with presence/absence as response variable were used for both, macro and microhabitat analysis. For the spatial analysis, a count of signs per quadrant was performed in each wetland and their distribution was evaluated by means of goodness-of-fit tests to Poisson and negative Binomial distributions. At JRL, coypus use both identified environments: Edge of the Marsh (EM) and Inner Marsh (IM). There is no seasonal variation with the exception of spring where there was total absence of signs. No cover variables were detected to predict presence. In the LG they only use the Middle Marsh (MM) environment, and not those of Edge (E) and Open Waters (OW). The probability of detection increases during autumn and winter and *Schoenoplectus californicus* was the main predictor species for the presence of signs. In both wetlands, signs were found in a clustered disposition. These results confirm the presence of coypu in the CPNP, with the JRL being a potential pathway into the park, and the MM of the LG being a key point of establishment. The environments used and the spatial arrangement of signs could be the result of the sustained food availability through seasons within the used environments, and protection from poaching and predation pressure. The seasonal variation partially coincides with the reproductive peaks previously observed in the wild for the species.

La presente investigación se desarrolló en los dos principales humedales del Parque Nacional Ciervo de los Pantanos (PNCP), Provincia de Buenos Aires, Argentina: Laguna Grande (LG) y Juncal del Río Luján (JRL). Los objetivos fueron: 1) Corroborar la presencia del coipo o falsa nutria, *Myocastor coypus* (Molina, 1782) dentro del parque, hasta el momento solo confirmada en la costa del Río Luján, y estudiar la variabilidad entre estaciones del año, 2) Evaluar el uso de hábitat del coipo y las variables potenciales que lo determinan mediante análisis a escalas de macro y microhábitat, y 3) Realizar estudios de disposición espacial de los signos de presencia de la especie. Estos dos últimos resultan fundamentales para comprender posibles procesos subyacentes, como la disponibilidad de alimento o respuesta a la histórica presión de caza. No solo se buscó responder cuáles ambientes de cada humedal utilizan, sino de qué manera lo hacen. Las hipótesis fueron: 1) Los sitios con presencia de signos varían entre estaciones, 2) Los sitios con presencia de signos dependen del tipo de cobertura vegetal, y 3) La disposición espacial de signos es agrupada. Se relevaron cuatro transectas en LG y tres en JRL mediante el método de línea transecta. En cada una se georeferenciaron sitios con y sin signos, se midieron variables de cobertura de diferentes especies vegetales (en %) y profundidad del agua (en cm). Tanto para macro como microhábitat se plantearon modelos lineales generalizados mixtos (GLMM) con presencia/ausencia como variable respuesta. Para el análisis de espacialidad se realizó un recuento de signos por cuadrante en cada humedal y se evaluó su distribución mediante pruebas de bondad de ajuste a distribución de Poisson y Binomial negativa. En JRL los coipos usan los dos ambientes identificados como Borde del Juncal e Interior del Juncal. No hay variación estacional, a excepción de la primavera donde hubo ausencia de signos. No se detectaron variables de cobertura que permitan predecir la presencia. En la LG solo utilizan el ambiente de Juncal Interior, y no los de Borde y Aguas Abiertas. La probabilidad de detección aumenta durante el otoño e invierno y la totora o junco, *Schoenoplectus californicus*, fue la principal especie predictora de la presencia de signos. En ambos humedales los signos se encuentran agrupados. Estos resultados confirman la presencia del coipo en el PNCP, siendo el JRL una potencial vía de ingreso al parque, y el Juncal Interior de la LG un punto clave de establecimiento. Los ambientes utilizados y la disposición espacial de signos podría ser resultado de la sostenida disponibilidad de alimento en donde fueron detectados, y de protección ante la presión por caza furtiva y depredación. La variación estacional coincide parcialmente con los picos reproductivos, observados previamente en estado silvestre para la especie.

Keywords: multi-scale study; Paraná River; populations; Rodentia; wetlands.

Introduction

The coypu, *Myocastor coypus* (Molina, 1782) is considered of special value by society for being a representative and conspicuous species of the wetlands (Administración de Parques Nacionales 1999). This species is a semi-aquatic rodent native to South America with gregarious habits (Guichón *et al.* 2003a). Its peak of activity occurs during crepuscular hours when it spends approximately 60 % of its time foraging (Salas *et al.* 2022) with a diet consisting mostly of rooted and floating vegetation present in the wetlands (Borgnia *et al.* 2000; Guichón *et al.* 2003b), although in some cases they may also consume grasslands vegetation relatively close to bodies of water (Galende *et al.* 2013; Hong *et al.* 2016). In terms of reproduction, it requires a minimum water level for copulation, and as a polyestrous species, multiple reproductive events can be detected throughout a year (Spina *et al.* 2009; Courtalon *et al.* 2011; 2015; with litters averaging between 3 - 6 individuals, and a range of 1 - 12 (Gosling 1981; Courtalon *et al.* 2015; Porini *et al.* 2019). Individuals can be detected directly by visualization, or indirectly by the presence of signs such as platforms, trails, caves, footprints, feces or chewed vegetation. The platforms are built with vegetation, which they weave for resting, but the females also use them to give birth. Trails are spaces left between the floating and rooted vegetation, as a coypu swims (Porini *et al.* 2019).

Although categorized as Least Concern by the Secretaría de Ambiente y Desarrollo Sustentable de la Nación (SAyDS) and Sociedad Argentina para el Estudio de los Mamíferos (2019), coypu populations have been under strong hunting pressure within its distribution in Argentina, being commercially the main wild mammal species for the value of its fur and meat (Colantoni 1993; Bó *et al.* 2006, 2013). Several authors have studied habitat use and population parameters of the coypu in areas under hunting pressure to better understand how the species may be affected (Arias *et al.* 2005; Guichón and Cassini 2005; Bó *et al.* 2006; Cruz Pinzón and Courtalon 2017). How this species responds to that pressure, however, is still a question pending to be answered, and studies involving explicit spatial data, such as this one, may help to elucidate.

Manly *et al.* (1993), proposes that habitat use may vary among different spatial scales. Therefore, it is important to define them clearly. The term "macrohabitat" is used to define the area where organisms carry out their biological functions and where their area of action is included. At this scale, different types of environments are often considered, such as forests, grasslands or flooded areas, among others (Maitz and Dickman 2001). The "microhabitat", on the other hand, refers to the physical and biotic conditions that influence the development of organisms and is expressed in the distribution of their activities within the

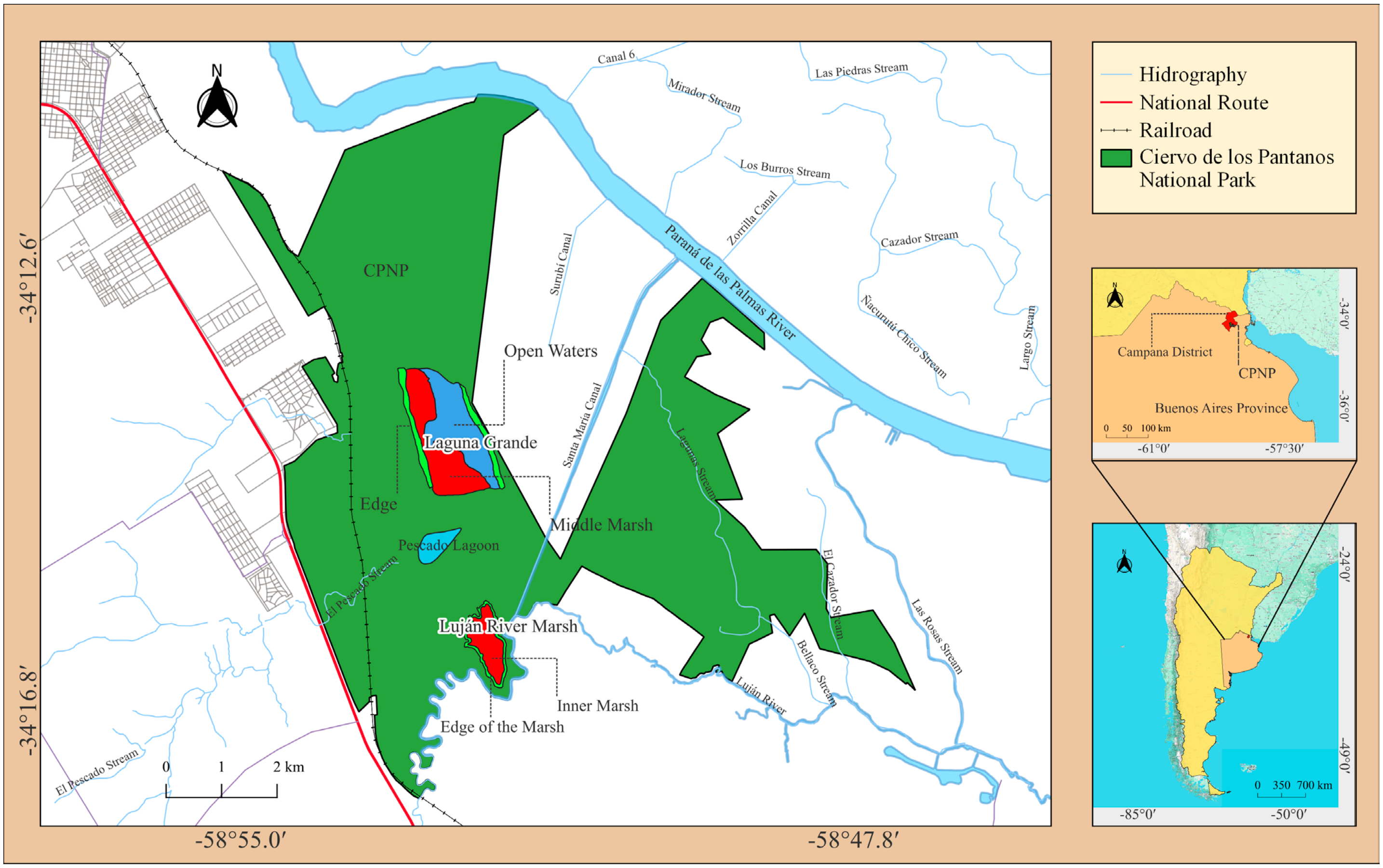

Figure 1. Map of Ciervo de los Pantanos National Park. Surveyed wetlands and its environments shown: "Laguna Grande" and "Juncal del Río Luján". Modified from Gabriela Gerardo (GIEH-FCEN-UBA).

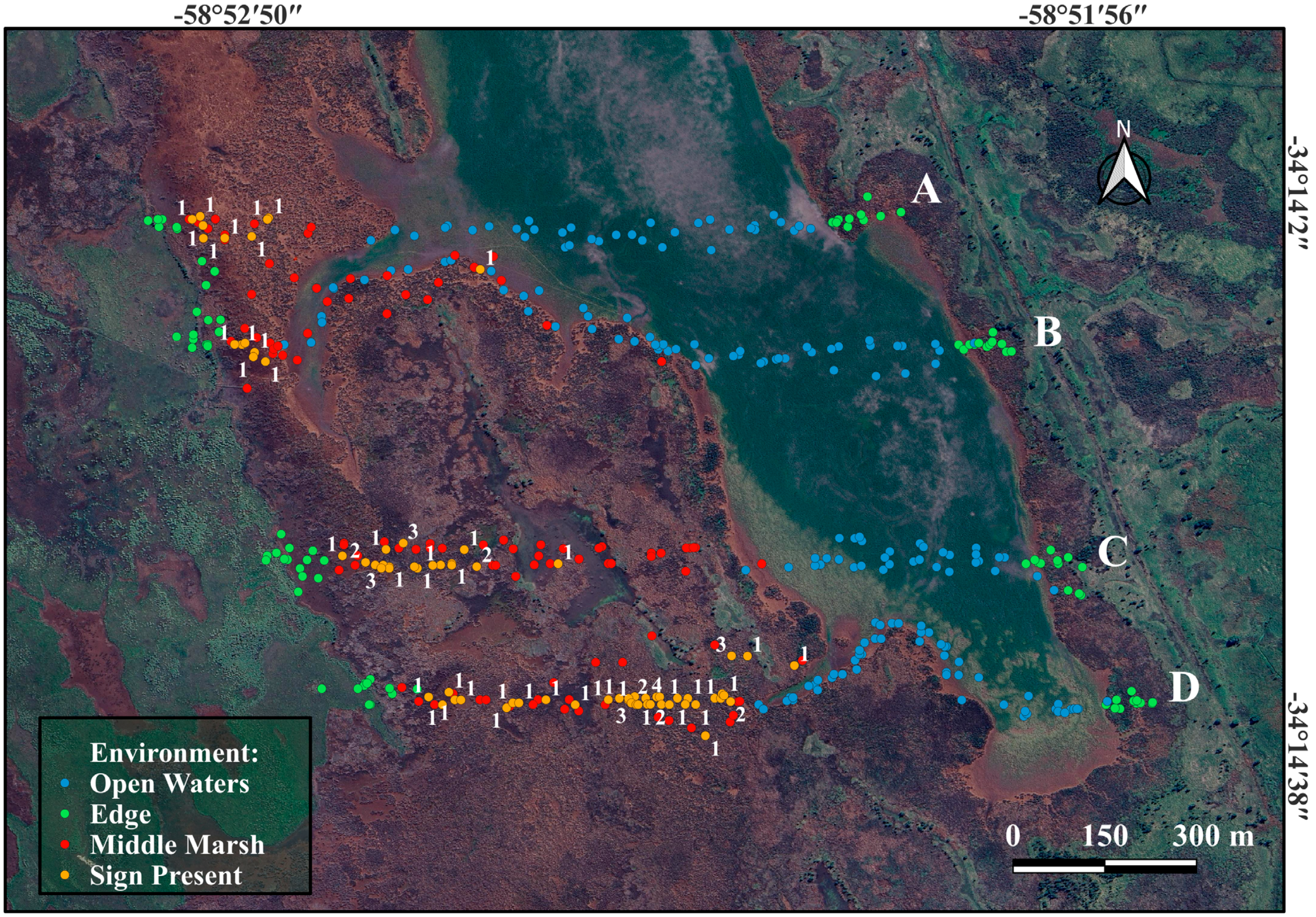

Figure 2. Accumulated point cloud of the surveyed transects during all four seasons in Laguna Grande wetland of the Ciervo de los Pantanos National Park. Transects (A, B, C and D) and points per environment are identified, highlighting in orange those where signs of presence were found, with the total number of signs found in each one written next to them.

macrohabitat. Therefore, habitat use is a multi-scale process and is a consequence of two decisions: first, where to live and establish the area of action, and second, what portion of that macrohabitat is used during daily activity (Johnson 1980; Orians and Wittenberger 1991).

The study and description of spatial patterns are central to decision-making in conservation biology (Primack 2006; Moilanen *et al.* 2009). One particular pattern, the "clustered" type, implies that individuals are grouped in clusters or patches, leaving portions of space relatively unoccupied. This pattern, so common in nature, may occur as a consequence of abiotic factors, social interactions, reproductive habits, resource availability or in response to human pressure.

Although numerous studies have been carried out along the Luján River (D'Adamo *et al.* 2000; Guichón et al. 2003a,b; Guichón and Cassini 2005, 2007), which marks the southern boundary of Ciervo de los Pantanos National Park, no studies have been conducted in two of its biggest wetlands, Laguna Grande (LG) and Juncal del Río Luján (JRL) (Figure 1). According to Guichón and Cassini (2007), who studied the habitat use by the coypu and classified the park boundaries within the "protected zone" of the Luján river, 100% of the sampled transects were positive for the presence of the coypu. Nevertheless, these transects only covered a maximum distance of 50 m perpendicular to the Luján river margin, without including the JRL or the LG.

The general objective of this work was to confirm the presence and evaluate the habitat use of the coypu in the main wetlands of the CPNP and the potential variables that determine it, as well as to generate a new source of valuable information for the park's management decisions regarding the protection of this species. The specific objectives for each studied wetland were as follows: 1) To analyze the habitat use at a macrohabitat scale; 2) To evaluate the potential association of sites with coypu presence in the CPNP to vegetation cover; 3) To describe the spatial distribution of coypu signs in the PNCP by integrating the information from points 1 and 2. Finally, the hypotheses derived from these objectives were 1) sites with and without signs of presence in the different environments will vary among seasons; 2) sites with use signs will be associated with the type of vegetation cover, and 3) the spatial arrangement of the sites with signs responds to a clustered distribution.

Materials and methods

I) Study area. The environments of the "Ciervo de los Pantanos" National Park (CPNP) are distributed in two large geomorphological units, called "High terrace" and "Low terrace", separated from each other by a ravine or paleo-cliff. The soil complex of the latter is characterized by having poor drainage, since it occupies low slopeless areas, known as marshes. It is in this area where the main wetlands are located: 1) "Laguna Grande", a large wetland covering the largest area of the park, and the reason why the CPNP is considered a "Wetland of International Importance or Ramsar Site (Secretaría de la Convención de Ramsar, 2013)", 2) The largest marsh of Luján River, located at the extreme south of the park, and 3) "Laguna del Pescado", located between both of the previously mentioned, although this last one wasn't included within the study for logistical reasons (Figure 1). These wetlands are a result of the geomorphology of the area and the base level imposed by the Río de La Plata, and are mainly maintained by groundwater from the aquifers and local precipitation that recharge the close to ground level phreatic surface. It is also regulated by the fluctuations and floods of the Paraná River, the Luján River, and by the contribution of streams such as the "Pescado" and "Otamendi" that come from the high terrace, cross the ravine, and discharge into the low terrace. Surface runoff is limited and the area remains periodically or permanently flooded (Administración de Parques Nacionales 2016).

The first site, Laguna Grande, was located on the lower terrace of the CPNP (34° 14′ 11.48″ S; 58° 52′ 26″ W), with an approximate extension of 156 ha (Rodríguez and Pizarro 2007). Based on a preliminary sampling carried out in July 2011 and the biological knowledge of the species, three main groups of environments were identified in the LG wetland at the macrohabitat scale:

Edge (E): Both edges were defined as the 100 m strip perpendicular from the limit of the waterbody. These are characterized by containing both, species typical of the saline grassland such as *Juncus acutus* (spiny rush), *Distichlis spicata* (seashore saltgrass) and *Limonium brasiliense* (caspia), and also those typical of the flooded grassland: *Schoenoplectus californicus* (California bulrush), *Typha latifolia* (common cattail) and *Scirpus giganteus* (club-rush).

Middle Marsh (MM): Dominated by *S. californicus*, with medium abundance of *T. latifolia* and lesser of *S. giganteus*, amongst others. Due to its irregular shape, this environment had variable extension in the different transects. Within this heterogeneous environment, a micro-relief was observed in which low flooded areas, with floating species such as *Azolla filiculoides* (mosquito fern), *Pistia stratiotes* (water lettuce), *Lemna minuta* (least duckweed) and *Wolffiella oblonga* (saber bogmat), were differentiated from slightly higher areas with typical flooded grassland vegetation dominated by *S. californicus*.

Open waters (OW): Characterized by lacking cover of emergent herbaceous vegetation (except for scattered patches of species such as *S. californicus*), and with high variability in terms of floating macrophytes cover.

While both, E and most of the MM, were sampled on foot, the OW and the internal flooded parts of the MM were covered using a kayak given their low accessibility. Seasonal samplings were conducted between spring 2011 and winter 2012. The transect line method (Krebs 1999) was used, identifying the presence (confirmed by the identification of at least 1 sign) or absence, counting the total number of signs and registering the GPS coordinates every 30 mts. Four transects with an approximate length of 1 km each and 100 m minimum between them were drawn, and covered with a west to east orientation, located in such a way as to proportionally cover the different types of environments. All of them were repeated throughout the four seasons, with samplings carried out within a maximum of 2 consecutive days. Signs were classified into three types: platforms (used to satisfy shelter and breeding requirements), chewed vegetation (indicators of feeding sites) and trails (signaling movement and potential feeding sites). Feces were not included due to their low detectability as a consequence of the constant fluctuation of the water level. When accessibility permitted, the longest and shortest platform diameters were measured. A Garmin® GPSmap 60CSx model was used to record the location of the points within the lagoon.

The second site, Juncal del Río Luján was located on the southernmost region of the park, adjacent to the Luján River (34° 16′ 35.10″ S; 58 ° 51′ 55.50″ W), and has been described according to the plant communities by Chichizola (1993). This section was classified by Guichón and Cassini (2007) as the "protected area" of the "deltaic portion" of the Luján River, where more than 97 % of its extension is included within three natural protected areas, one of them being the CPNP. This section, accessible only by navigation on the Luján River or an extensive hike in complex terrain, has low anthropogenic disturbance of its riparian environment (Guichón and Cassini 2007).

With regards to the vegetation that characterizes this section, it can be divided into two types of well-differentiated plant communities. On the one hand, there is the river ravine covered by a mixed grassland of *Sporobolus pyramidatus* (whorled dropseed) and *Xanthium cavanillesii* (Italian cocklebur). On the other hand, the inner marsh is a mosaic of *S. californicus*, *T. latifolia* and *S. giganteus* as the dominant species (Chichizola 1993). The edge of the marsh was considered as a transition zone between these two, containing a mixture of vegetation from the two environments. Samplings were conducted for each season of the year from summer 2013 to spring 2013. Based on a preliminary sampling conducted in this section of the park, in October 2012, it was determined that two different environments would be considered in this wetland at the macrohabitat scale: the Edge of the Marsh (EM) and the Inner Marsh (IM). Two transect lines with a maximum length of 345 m and separated by 50 m were covered at each season (A and B). However, due to the harsh conditions, a third transect (C) was covered in replacement of A, during one season. We defined EM as the transition zone corresponding to 25 % of the total length of each transect. The rest of the points correspond to the IM. At these points, separated by 15 mts, signs of coypu presence (platform, chewed vegetation, and footprints) were recorded. When accessibility permitted, the longest and shortest platform diameters were measured. The same Garmin® GPS GPSmap 60CSx model was used to record the location of the points.

II) Microhabitat scale. At each of the points surveyed within the transects, several variables were recorded in addition to the signs present:

I. The percentage cover of the dominant plant species was estimated using the Braun-Blanquet method within a 5 m radius from the point (Matteucci and Colma 1982).

II. The water depth at each of the points using the same graduated rod in all measurements in the center of the GPS point.

III) Spatial arrangement. Using QGIS Firenze 3.2.8 software, the cloud of georeferenced points was projected. Two grids containing 140 x 100 mts and 40 x 40 mts quadrats were used in LG and JRL respectively, in order to count the total number of signs observed per quadrat. These cell sizes were chosen due to the fact that the length of the transects differed between wetlands, as did the distance between points. Nevertheless, both scales represent significant areas for sign counts, and are proportional to the dimensions of the total surveyed area of each wetland. In LG wetland, only MM quadrats with at least 1 point (with or without sign presence) were included in the analysis. All quadrats fallen in OW and E were discarded given that only 1 sign was found present in the first one and none in the latter. We worked with a total of 48 quadrats where 95 signs were found to be present. In the JRL wetland, EM and MM quadrats were analyzed following the same criteria, with a total of 33 quadrats in which 17 signs were found. In both wetlands, data from all 4 seasons were analyzed together.

Statistical Analysis

1) Macrohabitat. At the macrohabitat scale, different generalized linear mixed models (GLMM) with presence/absence of signs as response variable were evaluated using the "glmmTMB" package (Brooks et al. 2017) of RStudio 4.3.2 (R Core Team 2023). Transects were identified as a random factor to declare lack of independence. Four models were tested in the two wetlands: Null (M0), Environment (M1), Environment+Season (M2) and Environment*Season (M3). In JRL wetland, spring data was not included in the analysis due the absence of signs. For the same reason, those of the E environment in LG were also excluded. A total of 369 points were evaluated in the LG and 119 in the JRL wetlands of the CPNP. Models were compared by Akaike's criterion, selecting the one with the lowest AIC. Finally, probability of presence for each environment was estimated for the final models using the "emmeans" package (Lenth 2023).

2) Microhabitat. At the microhabitat scale, multiple GLMMs with presence/absence of signs as a response variable were explored using the "glmmTMB" package (Brooks *et al*. 2017) of RStudio 4.3.2 (R Core Team 2023). Transects were identified as a random factor to declare lack of independence in the model. Models included different combinations of plant species cover (%) and water height surveyed at each point, as well as seasons as a four-level categorical variable (Summer, Fall, Winter and Spring). These were compared by Akaike's criterion, selecting the model with the lowest AIC. The assumptions of the selected model were evaluated with the DHARMa package (Hartig 2022). Once the model was selected, post-hoc contrasts were performed with the "emmeans" package (Lenth 2023) and model predictions were estimated with the "ggeffects" package (Lüdecke *et al*. 2020). In total, 448 points were evaluated in LG and 160 in JRL of the CPNP.

3) Spatial arrangement. Using "fitdistrplus" package (Delignette Muller and Dutang 2015) of RStudio 4.3.2 (R Core Team 2023) the distribution of observed signs was evaluated by goodness-of-fit tests to Poisson (random arrangement) and Negative Binomial (clustered arrangement) distributions by maximum likelihood method (Krebs 1999). Morisita's index (Krebs 1999) was also calculated for the two wetlands using the observed frequencies for each category of total sign counts per quadrat.

Results

1A) Laguna Grande Macrohabitat. A total of 448 points were surveyed, 79 corresponding to E, 193 OW and 176 MM (Table 1; Figure 2). Out of the total 448 points, 72 resulted positive for signs. Since no signs were found in environment E, points surveyed in this sector were removed from the GLMM, since the probability of presence is null and reduces the predictive capacity of the model. The 4 models (M0, M1, M2 and M3) were evaluated, and interaction between environment and season was determined to be not significant ($P > 0.05$). The additive model (M2) involving seasons and environments resulted in the lowest AIC (M0 = 366.25; M1 = 249.07; M2 = 222.12; M3 = 226.87). The final model compares the OW (193 points) and MM (176 points) environments at the 4 sampling seasons.

Table 1. Number of points with signs according to the season of the year for each environment of both studied wetlands: Laguna Grande and Juncal del Río Luján.

	Laguna Grande				**Juncal del Río Luján**		
	E[1]	**MM[2]**	**OW[3]**	**Total**	**EM[4]**	**IM[5]**	**Total**
	[79][6]	**[176]**	**[193]**	**[448]**	**[39]**	**[121]**	**[160]**
Summer	0 (0)[7]	13 (13)	0 (0)	13 (13)	0 (0)	4 (5)	4 (5)
Autumn	0 (0)	25 (35)	1 (1)	26 (36)	2 (4)	2 (2)	4 (6)
Winter	0 (0)	28 (38)	0 (0)	28 (38)	1 (3)	2 (3)	3 (6)
Spring	0 (0)	5 (9)	0 (0)	5 (9)	0 (0)	0 (0)	0 (0)
Total	0 (0)	71 (95)	1 (1)	72 (96)	3 (7)	8 (10)	11 (17)

1: Edge; 2: Middle Marsh; 3: Open Waters; 4: Edge of the Marsh; 5: Inner Marsh 6: Total points surveyed per environment between square brackets; 7: Number of points with present signs and total number of signs between regular brackets.

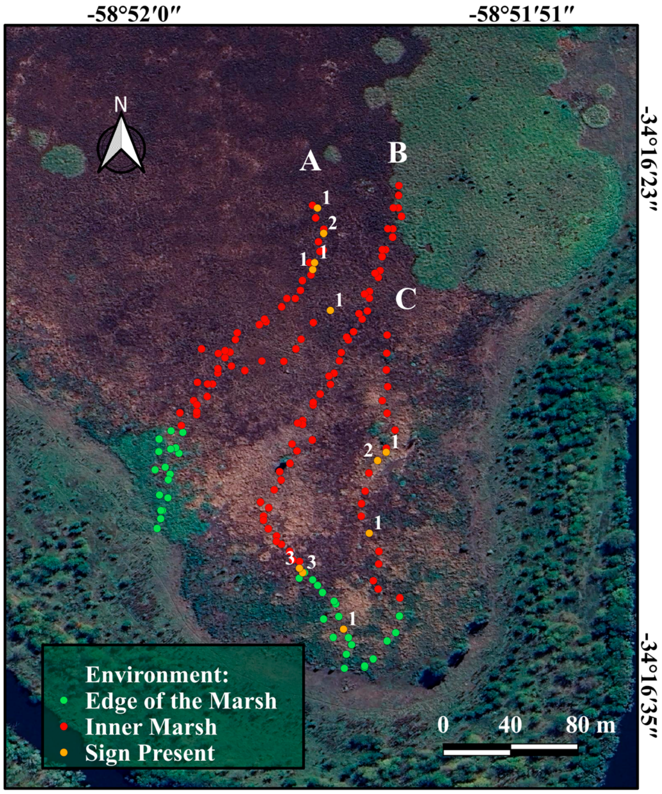

Figure 3. Accumulated point cloud of the surveyed transects during all four seasons in Juncal del Río Luján wetland of the Ciervo de los Pantanos National Park. Transects (A, B, C) and points per environment are identified, highlighting in orange those where signs of presence were found, with the total number of signs found in each one written next to them.

Significant differences were found between both environments ($P < 0.0001$) and between seasons. Given no interaction was detected, a posteriori contrasts by Tukey's method were performed only for main effects. The estimated probabilities of sign presence were estimated between [0.0004; 0.024] and [0.24; 0.49] for OW and MM, respectively. On the other hand, values between [0.03; 0.29], [0.03; 0.26], [0.002; 0.04] and [0.006; 0.07] were estimated for winter, autumn, spring and summer seasons respectively, with no significant differences between winter/autumn or spring/summer ($P = 0.58$; 0.99), but significant indeed between winter or autumn with respect to spring ($P = 0.0004$; 0.0003) or summer ($P = 0.002$), indicating that the probability of signs presence increases during cold seasons.

Platforms accessible for measurements were analyzed. During spring 2011 (n = 3) were woven solely with *S. californicus*, in an approximately elliptical shape, with an average large diameter of 40 cm and a smaller one of 30 cm. During summer low accessibility to the platforms did not allow recording their measurements. In autumn 2012, 31 platforms were analyzed, of which only one was knitted with *T. latifolia*, while the remaining ones were with *S. californicus*. These exhibited highly variable measurements, with an average long diameter of 49.68 ± 22.13 cm and a short one of 35.48 ± 20.99 cm. In winter 2012, 8 platforms were measured, all of *S. californicus* with a less elliptical shape than in the other seasons. The average large diameter resulted in 47.50 ± 19.09 cm and the smaller one 41.25 ± 16.42 cm.

1B) Juncal del Río Luján macrohabitat. A total of 160 points were surveyed, 39 corresponding to EM and 121 to IM. In JRL, signs were found in both environments (Table 1; Figure 3). Data collected during spring (41) were left out of the analysis due to the total absence of signs, so only the 119 points left from the remaining seasons were used. Assessing the M3 model no interaction between environment and season was found, and the model with the lowest AIC resulted to be M1, which only included the environments (M0 = 90.14; M1 = 89.7; M2 = 92.89; M3 = 91.84). No significant differences were found among IM and EM environments ($P = 0.7$), with estimated presence probabilities of [0.04; 0.16] and [0.03; 0.29] respectively. It should be noted that the signs found in both, EM and IM, correspond solely to platforms (17). Five of them were measured during summer, six in autumn and six in winter. Their average long diameters were [53.43 ± 10.77 cm], [47.56 ± 11.35 cm] and [47.60 ± 7.43 cm] respectively, while their short ones were of [33.44 ± 1.5 cm], [33.50 ± 4.78 cm] and [41.70 ± 2.21 cm].

It is crucial to note that the wet period during the year under study lasted from January to April, including summer and part of autumn 2013. While the driest stage was observed from May to December 2013, with a low annual accumulated rainfall of 293.8 mm. The highest flood for the Lujan River was 5.10 m, recorded in November 2012 prior to the start of the sampling period.

2A) Laguna Grande microhabitat. Two models were initially proposed: a null model containing no covariates at all, and another that included the water depth (cm) and cover of the dominant plant species: *S. californicus*, *T. latifolia*, *Chenopodium* spp. and floating macrophytes (*L. minuta*, *P. stratiotes* and *A. filiculoides*). A possible interaction between *S. californicus* cover and seasons was detected in the exploratory analysis, so not only additive models were evaluated, but also this interaction was considered. Following the selection methodology previously described, the final model presented below (in the linear predictor scale) was selected. This model includes the variables of *Chenopodium* spp. and *S. californicus* cover, seasons, and interaction between *S. californicus* cover and seasons as explanatory variables that were found significant in order to predict the probability of the sign's presence in LG.

The final model proposes that *S. californicus* cover is the main variable able to predict the probability of coypu signs presence in the LG wetland, being this relation positive. However, it is observed that when adding seasons as a categorical variable to the model, presence as a function of *S. californicus* cover is dependent on the season (Figure 4a). Due to the fact that the final model includes two vegetation cover variables (continuous), in order to evaluate differences between seasons (categorical) while accounting for the interaction, contrasts were performed by fixing cover values of *Chenopodium spp.* at 0 % and *S. californicus* at both extreme (0 and 100 %) and mean cover values of the observed data (33.2 %). Contrasts revealed that

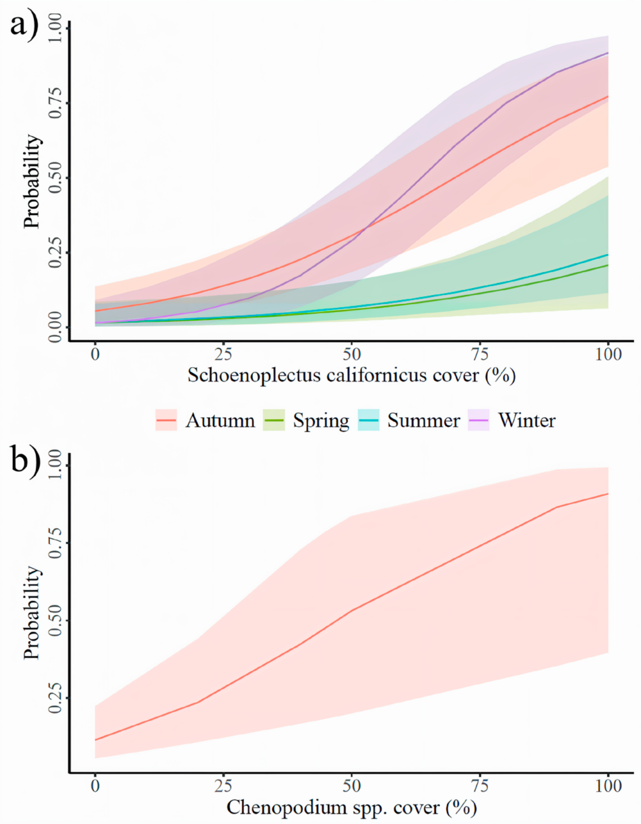

Figure 4. Predicted probabilities of coypu signs presence in Laguna Grande wetland as a function of: a) *Schoenoplectus californicus* cover (%) for each season; b) *Chenopodium spp.* cover (%), for all seasons. Each prediction is presented with its respective confidence interval (α = 0.05).

signs presence increases significantly in autumn and winter compared to summer and spring seasons (all $P < 0.0001$), when cover of *S. californicus* is maximum. Meanwhile, for a mean cover of 33.2 %, it is significantly higher solely in autumn with respect to spring ($P = 0.04$) and summer ($P = 0.04$) but no different than winter ($P = 0.85$), and no differences were detected with 0% cover (all $P > 0.99$). Therefore, a high probability of signs detection is expected for LG in winter and autumn, with predicted values of [0.76; 0.98] and [0.54; 0.91] respectively, while in spring and summer these values are lower and more variable with [0.06 %; 0.50] and [0.11; 0.44] respectively, when cover of *S. californicus* is maximum.

Chenopodium spp. cover was also significant ($P = 0.0012$), although with an imprecise confidence interval. This is due to the fact that of the total number of sites analyzed (448) only 8 registered high cover of this species. However, given that 3 of them showed clear signs of presence the model is sensitive enough to detect that there is an increasing trend in the probability of presence of coypu signs as a function of higher cover of *Chenopodium* spp. in LG (Figure 4b). Probabilities of sign presence are estimated between [0.06; 0.22.], [0.20; 0.84] and [0.40 ;0.99] for covers of 0, 50 and 100 % of *Chenopodium* spp. respectively.

A total of 96 signs were recorded, consisting of 89 nests/platforms (92.7 %), 4 chewed vegetation (4.16 %) of *S. californicus* and 3 trails (3.125 %) in *Chenopodium* sp.

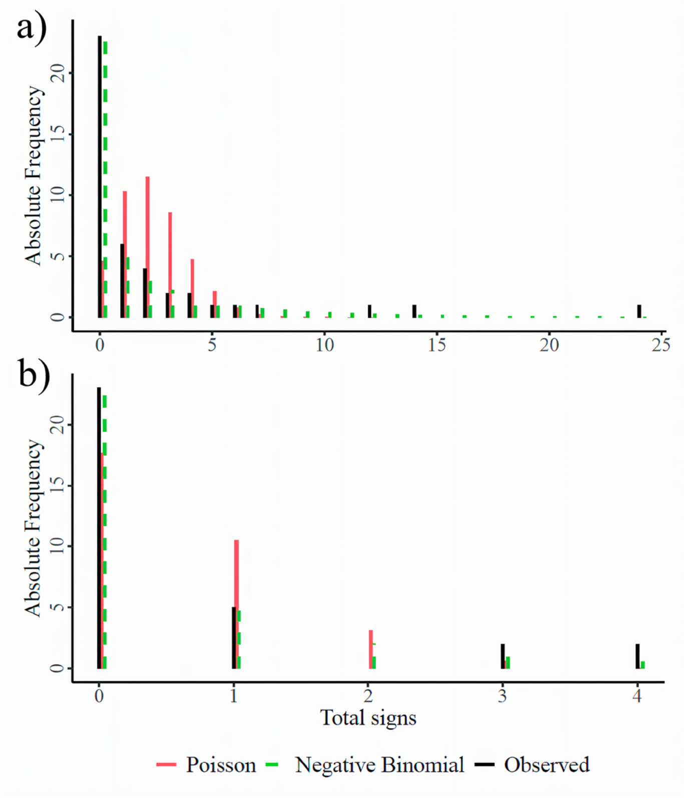

Figure 5. Comparison between the observed and theoretical Poisson and Negative binomial sign frequency distributions in: a) Laguna Grande wetland; b) Juncal del Río Luján wetland.

The OW environment presented small patches of *S. californicus* with a mean percentage cover of [15.75 ± 23.92 %]. Floating macrophytes such as *L. minuta* or *A. filiculoides* showed high seasonal variability, with percentage covers of [5.77 ± 13.02 %] and [1 ± 5.43 %] for winter and autumn respectively, while in summer and spring these values increase notably to ranges between [41.96 ± 44.90 %] and [48.57 ± 46.21 %]. In contrast, the IM presented a mean cover of [54.54 ± 45.76 %] for *S. californicus*, while floating macrophytes had were more stable amongst seasons with minimum cover in winter of [8.9 ± 20.5 %] and maximum in summer of [33.25 ± 30.84 %]. The E environment presents a *S. californicus* cover of [21.4 ± 33.7 %]. However, the cover of floating macrophytes was low or null with values of [5.6 ± 18 %].

2B) Juncal del Río Luján microhabitat. Following the same steps in the JRL wetland, 2 models, one null and another including the cover of *S. californicus*, *S. giganteus*, *T. latifolia*, *Hydrocotyle bonariensis* (largeleaf pennywort) and the seasons were initially proposed. Water height was not included due to lack of data as a consequence of the dry season. No interaction between seasons and *S. californicus* cover was observed ($P > 0.05$). In the selection process, the model with the lowest AIC was the one that only retained the *S. californicus* cover variable.

However, despite being quite a simple model due to having just one explanatory variable, SC coefficient was not significant ($P = 0.15$), indicating that no variable measured in the JRL could clearly predict coypu signs presence.

3A) Laguna Grande Spatial arrangement. The Poisson distribution hypothesis was rejected (Chi = 84.95; $P < 0.0001$), so no random arrangement of signs was detected (Figure 5). On the other hand, the negative binomial distribution hypothesis was not rejected (Chi = 0.068; $P > 0.79$). The empirical frequency distribution compared to the theoretical frequency distributions expected with the observed data show that the sign arrangement of this species in the MM of LG is clustered (Figure 5). The Morisita index was 38.13, which is also consistent with a clustered arrangement.

3B) Juncal del Río Luján Spatial arrangement. The Poisson distribution hypothesis was rejected (Chi = 4.489; $P = 0.03$), so no random arrangement of signs was detected (Figure 5). The negative binomial distribution goodness of fit p-value could not be evaluated due to lack of freedom degrees as a consequence of the low sign counts in this wetland. However, the empirical frequency distribution compared to the theoretical frequency distributions expected with the observed data suggest that the sign arrangement of this species in the JRL wetland could be clustered (Figure 5). Consistent with this, the Morisita index took a value of 10.87.

Discussion

Signs detected within the surveyed environments of the two wetlands allow us to affirm that the coypu is present in the CPNP. Returning to the particular objectives and their derived hypotheses (H), the discussion of these results will follow an orderly manner analyzing first each of the wetlands studied and finally presenting a habitat use model for the CPNP.

Laguna Grande. The macrohabitat analysis allows us to affirm that the three environments surveyed are different in terms of signs presence. No signs were found in the E environment, although some were indeed located within the MM but close to its limits with E. With the exception of 1 found in OW, all signs were detected in the MM, clearly indicating that the latter is used by coypu over the other environments. Signs found were mostly sessile platforms, built on *S. californicus*, with the exception of 3 trails detected on *Chenopodium* spp. No trails or mobile platforms built on non-rooted floating macrophytes were detected. Despite offering small patches of *S. californicus* and availability of floating macrophytes such as *L. minuta* or *A. filiculioides* as food source (Borgnia *et al.* 2000; Guichón *et al.* 2003b), the OW environment remained unused at all seasons. If we compare with the MM, not only does the latter offer higher average cover of *S. californicus*, but also food availability is relatively higher during all of the seasons. On the other hand, the E environment presents sufficient cover of *S. californicus* for coypu to weave their platforms. However, both the low cover of floating macrophytes and the mean depth of 35.7 cm could be acting as a limiting factor. Porini *et al.* (2002) proposed that coypu populations use environments with high cover of species such as *S. californicus* not only for the direct usage as nesting sites, but also that the higher water depth within these sites might be a crucial factor for protection against predators by submersion (including humans). Guichón and Cassini (1999) reported that variables associated with human disturbance were the most negatively correlated with coypu presence. Hong *et al.* (2016) carried out isotope diet studies and determined that coypu may increase the consumption of terrestrial vegetation in order to cover their daily share when availability of macrophytes is scarce. All this being considered, proximity to the park trails (anthropic) and low water level may be a more suitable explanation to why the E environment remained unused, rather than food or nesting sites availability, given that coypu could consume terrestrial vegetation. Another important result of this analysis is the distinction between seasons, with higher signs of presence during autumn and winter compared to spring and summer. This, we believe is partially correlated with the reproductive functionality of platforms, built by adults to give birth (Porini *et al.* 2019). Previous works from Courtalon *et al.* (2015) identified autumn and spring as the calving peak seasons detected in wild areas, which in contrast with these results might suggest there are other factors such as forage vegetation availability determining the higher signs presence, especially during winter. This being said, it would be of interest to carry out reproductive studies of this species within the park, in order to further understand the factors determining both peaks. Finally, evidence obtained for this wetland does not support the H1, since there is no variation between environments, only seasonal variation independent from them.

On the other hand, evidence does support H2 at the microhabitat scale, since the final model proposes that *S. californicus* cover is the main plant cover variable, able to predict the presence of coypu signs in the LG wetland, this relationship being positive. However, it is observed that when adding seasons as a categorical variable to the model, sign presence probability as a function of *S. californicus* cover is dependent on the season (Figure 4), consistent with the results obtained at the macrohabitat scale. Models shown in this study resulted in significantly higher presence for autumn and winter rather than summer and spring seasons under 100 % cover of *S. californicus*, while for a mean cover of 33.2 % it is only significantly higher in autumn. Diet studies carried by *Galende et al. (2013)* in a steppe lagoon in Argentine Patagonia demonstrated that coypu was a selective consumer, with its diet consisting primarily of *Myriophyllum* sp. (submerged macrophyte) and *S. californicus*, also with variation between seasons. Borgnia *et al.* (2000) also made microhistological feces analysis and determined that *Lemna* sp. (floating macrophyte) was the main diet component, especially during summer and spring seasons. As previously stated, winter season has the lowest availability of floating macrophytes, so *S. californicus* selection as a potential feeding component may explain the peaks observed. Also, it may be suitable for explaining why despite the presence of other emergent herbaceous vegetation species such as *T. latifolia*, coypu selected *S. californicus* over any other species in the LG wetland. Another plant species used that appears in this environment is the aforementioned *Chenopodium* sp. where coypu trails were found. Considering that during 60 to 80 % of the time spent outside their shelters, coypu actively feed on vegetation while moving (Guichón, 2003a; Salas *et al.* 2022), it is likely that this species is used for foraging, although it would be interesting to carry out diet studies to confirm this.

To test H3, a spatial analysis was carried out exclusively contemplating the MM environment, since 95 of the 96 total signs were detected there. Under the results of both goodness-of-fit tests and the calculation of Morisita's index, evidence upholds in favor of H3, indicating a clustered distribution of signs in this environment. Looking at Figure 2, there are 4 clear clusters of signs (1 per transect), the main ones being those detected in transects C and D. This spatial pattern might follow after the fact that it could allow coypu to seek refuge from multiple threats present in their environment, as well as to maximize the resting and breeding area, while minimizing the effort required at the time of feeding. This result contributes evidence that supports the behavioral tradeoff hypothesis postulated (D'Adamo *et al.* 2000; Borgnia *et al.* 2000; Gosling 1981). Domestic predators such as dogs or other natural predators such as birds of prey, ophidians (yararás) are found on the E, since it is a transitional environment between this large wetland and the saline grassland of the CPNP where these species occur. Another important problem for this species within the park is the hunting pressure exerted by poachers who enter illegally outside visiting hours (Cruz Pinzón and Courtalon 2017; Courtalon *et al.* 2019). In other words, the pressure over coypu in the CPNP is not only one of natural origin, but also anthropogenic. Therefore, in addition to what has been discussed regarding E at the macrohabitat scale, the absence of signs in this environment not only is reasonable, but also it may be one of the leading factors for coypu to seek for protection in a more isolated environment, and more suitable for their regular activities, such as the MM.

Juncal del Río Luján. At the macrohabitat scale, results show that coypu uses the 2 surveyed environments. Only platforms woven with *S. californicus*, *T. latifolia* or *S. giganteus* (species noted for their great height), were found on the Edge of the Marshand (EM) and Inner Marsh (IM) environments. As previously stated, the presence of this type of vegetation is essential for the establishment of a coypu population, since these use mainly emergent herbaceous vegetation such as the above mentioned to weave breeding and resting platforms (Borgnia *et al.* 2000; Porini et al. 2002, Bó *et al.* 2006). The presence of signs in both environments lead us to suppose that the Juncal del Río Luján is an entryway to the CPNP, and that the coypu use not only the coast of the river (D'Adamo *et al.* 2000; Guichón and Cassini, 2007), but also both, a transitional environment such as the EM, and one with a proper wetland vegetation physiognomy such as the IM. As far as the seasons are concerned, no differences were detected, except for spring, where the absence of signs was total. Given that the JRL wetland is located within the Luján River flood valley, the influence of hydrological dynamics is essential for this environment to remain saturated with water, either by direct precipitation or by the overflow of the river during floods (Comité de Cuenca del Río Luján, 2013). We believe that these results are related to the hydrological dynamics of this year, characterized by a strong drought. Such was its magnitude that, from July to December 2013, total cumulative rainfall was recorded below 60 mm and there was a single flood event of the river, reaching barely a maximum of 2.7 m, well below the 5.1 m recorded in the pre-sampling at the end of 2012 (Data from Servicio de Hidrografía Naval). Therefore, the signs present during the previous seasons (summer, autumn and winter of 2013) would be expected to belong to individuals that arrived with the floods prior to the beginning of the sampling season. In turn, their disappearance in spring, the last season surveyed, would be due to the lack of a minimum water level required to carry out their activities normally, especially reproductive ones.

With all the above mentioned, the information gathered does not support H1, since no variation was detected in the sites with signs between environments throughout the seasons, except for the particular case of spring.

Results at the microhabitat scale were inconclusive, as no vegetation or environmental variable was found to clearly predict the presence of coypu signs. For this reason, more information should be collected in order to study H2 within this wetland. It is possible that this result is due to two main reasons. First, the low number of signs detected in the total number of points surveyed in the 4 stations (17 out of 160), mainly because it was an extremely dry year, water being the limiting variable for coypu reproduction and survival (Bó *et al.* 2008; Porini et al. 2019). Secondly, most of the platforms found were woven with the dominant vegetation of this environment, *S. californicus*, so there are included in the analysis a large number of points with high cover of this species, but with no signs present, reducing the sensitivity of the model. Such is the dominance that the mean cover in EM and IM turned out to be [67.5 ± 35 %] and [72.3 ± 32.4 %] respectively. This brings us to the question of whether coypu actually selects *S. californicus* in this environment or whether its utilization is simply an availability response. To answer this and other questions, such as what happens in wetter seasons, this marsh, the most representative of the park, should be monitored seasonally.

To test H3, an implicit spatial analysis was performed to evaluate whether the arrangement of signs is random, regular or clustered. The results of the goodness-of-fit test allow us to reject a random arrangement of the signs, but the limited amount detected is not sufficient to properly calculate a p-value and evaluate whether it is indeed a clustered arrangement. However, complementing with the Morisita index whose value is 10.87 we can infer that there is an underlying clustering with two main focal zones: deep in the IM (northern end of the transects) and between both EM and IM (lower end of the transect) (Figure 3). In conclusion we assume that the signs are clustered as there is no statistical evidence to reject H3. It is important to remember that this analysis was performed with the total count of signs detected at each point, and not only with presence/absence.

Conclusions. Analyzing these results altogether, it is unmistakable that there is a resident coypu population present within both of the main CPNP wetlands, with a high probability of having active reproduction since the main signs detected consisted of platforms. In support of the behavioral tradeoff hypothesis, the clustering pattern in both wetlands could be a response of the species seeking shelter from potential threats present within the park. Also supporting this hypothesis is the fact that the Edge of LG remained unused while the Edge of the JRL was indeed used, being the first one directly connected with the park trails, while the second one is located in a more isolated area. In both wetlands, *S. californicus* was the main species used for weaving its platforms, which may be also an important food source when other resources such as *Lemna* sp. are scarce, especially during colder seasons. Nevertheless, as previously mentioned, this could be an availability response that requires further study to define whether or not it is positively selected. As for seasonal variation, clear differences were observed between the two wetlands. In LG, we found what seems to be a response mainly to reproductive peaks observed in wild environments (Courtalon *et al.* 2015), as no there were no clear limiting factors in terms of shelter or food availability observed between seasons in the MM environment. On the other hand, in the JRL wetland, differences between Spring and the rest of the seasons are highly likely to have occurred due to the influence of the hydrological regime on this wetland, fundamental in the surveyed year characterized by a strong drought.

Complementing with previous studies from D'Adamo *et al.* (2000), who detected coypu presence in the Lujan River Ravines within the park limits, this marsh located in the southernmost region of the CPNP could be an entryway for coypu to access to the other wetlands such as the LG. It would be interesting to include the Pescado Lagoon in future research, in order to further understand the connection between these three main wetlands.

Finally, we propose to carry out seasonal monitoring of the presence of this species in the park, and diet studies to help elucidate the underlying causes of these patterns of space use, observed for the coypu in the CPNP.

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