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Alan Lopes¹

alanlopes.bio@gmail.com

Universidade Federal do Rio Grande

Fabiana Schneck¹

Universidade Federal do Rio Grande

Eduardo R. Secchi¹

Universidade Federal do Rio Grande

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Habitat use patterns and diet of *Lontra longicaudis* (Olfers 1818) in urban streams of southern Brazil

Alan Lopes^{1,2}, Fabiana Schneck¹, Eduardo R. Secchi^{1,2}

¹ Programa de Pós-Graduação em Biologia de Ambientes Aquáticos Continentais (PPG-BAC), Instituto de Ciências Biológicas (ICB), Universidade Federal do Rio Grande (FURG), Rio Grande, Rio Grande do Sul, Brazil

² Laboratório de Ecologia e Conservação da Megafauna Marinha (ECOMEGA), Instituto de Oceanografia, Universidade Federal do Rio Grande (FURG), Rio Grande, Rio Grande do Sul, Brazil

Corresponding author: Alan Lopes

E-mail: alanlopes.bio@gmail.com

ORCID: <https://orcid.org/0009-0009-7463-726X>

Abstract: The Neotropical otter (*Lontra longicaudis*) is a semiaquatic mammal widely distributed throughout Latin America and is considered an important indicator of aquatic ecosystem integrity. This study evaluated the habitat use and feeding ecology of the species in three coastal streams in the municipality of Rio Grande, Rio Grande do Sul, Brazil, representing different levels of urbanization and landscape modification. Sampling was conducted monthly from August 2024 to July 2025 in three streams along an urbanization gradient. Indirect signs of the species were recorded, the microhabitats used were characterized, and land use and land cover surrounding the watercourses were analyzed using imagery obtained from an unmanned aerial vehicle and processed through supervised classification. Diet was determined through fecal analysis. Habitat-use intensity was estimated based on sign encounter rates, while spatial and seasonal differences were assessed using non-parametric tests and multivariate analysis (PERMANOVA). A total of 175 signs were recorded, most of them in the intermediate-urbanization stream (133), followed by the most urbanized (29), and the least urbanized (13). Encounter rates differed significantly among streams and were highest in the intermediate-urbanization stream, with no significant seasonal variation. Sandbanks accounted for 95.1% of all records, highlighting their importance both as marking sites and for sign detectability. Diet was predominantly composed of fish, followed by crustaceans and birds, with no significant differences in diet composition among streams or seasons. The results indicate that habitat-use intensity was more closely associated with the availability of favorable microhabitats, landscape connectivity, and anthropogenic disturbance than with riparian vegetation extent alone. We conclude that the conservation of Neotropical otter in anthropized coastal landscapes depends on maintaining functional connectivity among aquatic environments and mitigating the impacts of urbanization.

Keywords: Peri-urban environments; Semiaquatic carnivores; Landscape connectivity; Trophic ecology; Anthropogenic impacts; Urbanization.

Introduction

Mammals perform essential functions in ecosystems, contributing to processes such as pollination, seed dispersal, and population control (Galetti et al. 2022). In aquatic environments, semiaquatic predators play an important ecological role by regulating prey populations and responding sensitively to changes in water quality, resource availability, and bank habitat structure, thus being recognized as good indicators of ecosystem integrity (Kruuk 2006). Among them, the Neotropical otter, *Lontra longicaudis* (Olfers 1818), stands out as a widely distributed top predator in freshwater and coastal ecosystems of Latin America and is strongly associated with the

integrity of aquatic and riparian environments (Larivière 1999; Rheingantz et al. 2014; Lesage et al. 2025). The species has a broad geographic distribution, occurring from Mexico to northern Argentina and inhabiting different aquatic ecosystems, from sea level to mountainous regions (Larivière 1999; Rheingantz et al. 2014). Despite this broad distribution, its occurrence is closely associated with the availability of water bodies exhibiting abundant prey and high structural complexity along their banks. Elements such as continuous riparian vegetation, undercut banks, exposed roots, natural cavities, and meandering reaches provide sites for shelter, resting, movement, and territorial marking, and are considered fundamental for species persistence (Gallo-Reynoso 1997; Perinchery et al. 2011; Quintela et al. 2011). In contrast, anthropized environments reduce the availability of these structural elements, alter the composition of aquatic communities, decrease the abundance of sensitive prey, and favor generalist/opportunistic species, reflecting functional changes in the ecosystem and increasing the likelihood of conflicts between otters and human activities (Wong & Candolin 2015; Rheingantz et al. 2017).

Increasing land-use conversion and degradation of riparian habitats represent some of the main threats to semiaquatic predators globally (Rheingantz & Trinca 2015). As a consequence of these pressures, the Neotropical otter is currently classified as Near Threatened by the International Union for Conservation of Nature (IUCN), with habitat loss and degradation, pollution, hydrological alterations, and human-wildlife conflict recognized as the main factors driving population declines across its range (Reis et al. 2006; Barbieri et al. 2012; Rheingantz et al. 2021). Across its geographic range, the Neotropical otter exhibits a predominantly piscivorous and opportunistic feeding strategy, with fish representing the main prey, while crustaceans and other aquatic and terrestrial vertebrates may contribute variably according to local prey availability and environmental conditions (Rheingantz *et al.* 2017). In southern Brazil, studies conducted in coastal and inland aquatic systems consistently reported fish as the principal food item, with crustaceans becoming particularly important in areas influenced by coastal or brackish waters and other prey being consumed opportunistically (Colares & Waldemarin 2000; Quintela *et al.* 2008). In this context, understanding how environmental and anthropogenic factors influence the distribution and habitat use of the species is essential to support conservation strategies in increasingly modified landscapes (Barbosa et al. 2003; Perinchery et al. 2011; Prakash et al. 2012). In Brazil, studies on the Neotropical otter have focused mainly on describing its diet or characterizing its distribution and habitat use, generally addressed independently (Waldemarin & Colares 2000; Kasper 2004; Quintela et al. 2011; Sousa et al. 2013). More recently, some studies have incorporated environmental and anthropogenic variables to explain species occurrence, highlighting the influence of factors such as land use, vegetation cover, and proximity to roads on the spatial distribution of its signs (Andrade et al. 2019). However, studies simultaneously integrating patterns of

habitat use and diet in small water courses subjected to different levels of urbanization remain scarce, particularly in coastal systems.

The Holocene coastal plain of Rio Grande do Sul is characterized by low elevation, gently undulating terrain, and high connectivity among lagoons, wetlands, channels, and streams, forming a dynamic and ecologically relevant hydrographic network (Sfredo & Tagliani 2016). However, urban expansion has promoted the removal of marginal vegetation, channel straightening, bank erosion, and effluent discharge, all of which compromise the quality of habitats used by semiaquatic predators (Walsh et al. 2005; Sfredo & Tagliani 2016). Although these environments are likely important for the conservation of the Neotropical otter, they remain poorly studied, particularly regarding the combined effects of urbanization on food-resource availability and species occupancy patterns. The present study aimed to analyze how different levels of urbanization and anthropogenic impact influence the diet and intensity of habitat use of the Neotropical otter, over an annual sampling cycle, in three streams within the municipality of Rio Grande, a subtropical coastal plain region in southernmost Brazil.

Materials and methods

Study area

The study was conducted in three coastal watercourses located in the municipality of Rio Grande, state of Rio Grande do Sul, Brazil: the Bolaxa, Martins, and Cabeças streams. For the purposes of analysis and presentation of the results, the three watercourses were considered representative units of an urbanization gradient, with Bolaxa Stream (BolStr) classified as the least urbanized environment, Martins Stream (MarStr) as the intermediate-urbanization environment, and Cabeças Stream (CabStr) as the most urbanized environment. This classification was established based on land-use and land-cover context, marginal vegetation characteristics, and the degree of anthropogenic disturbance observed in each area. All three are located within the subtropical coastal plain of Rio Grande do Sul, a region characterized by a complex ecological mosaic of wetlands, salt marshes, inland lagoons, streams, dunes, grasslands, and forests, resulting in high biodiversity (Tagliani 2022). This plain is bounded by the waters of the southwestern Atlantic Ocean and the Patos, Mirim, and Mangueira lagoons, forming a hydrographic system of high ecological relevance (Fig. 1).

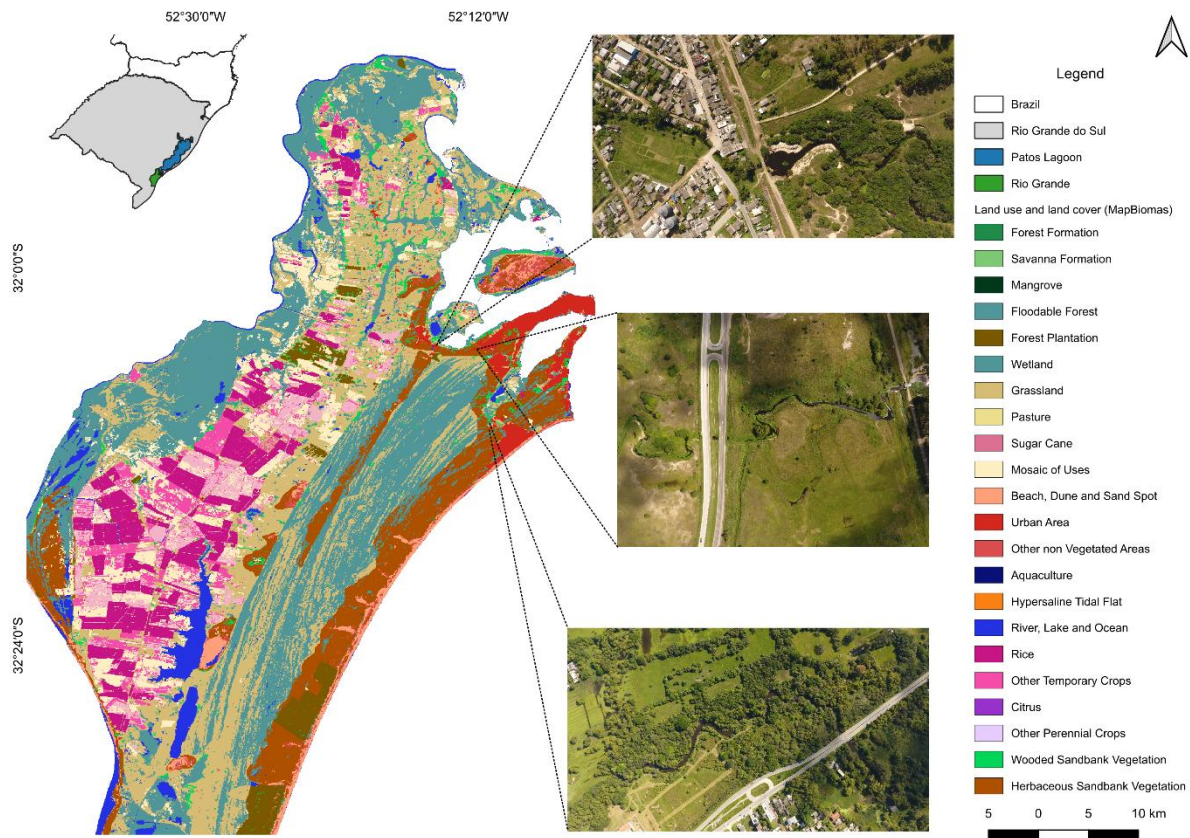


Fig. 1 Location of the municipality of Rio Grande, in southernmost Brazil, together with the study areas of the monitored streams (Cabeças, Martins, and Bolaxa streams), showing land use and land cover obtained from Collection 10 of the MapBiomas Project, based on the 2024 reference year. The classes represent different natural formations and anthropogenic areas, allowing visualization of the environmental context and the urbanization gradient associated with sampling effort. For comparative interpretation, the streams were classified into three urbanization categories: least urbanized environment (BolStr), intermediate-urbanization environment (MarStr), and most urbanized environment (CabStr). Black lines indicate the stretch surveyed along the watercourses.

According to Sfredo and Tagliani (2016), the formation of coastal ridges, also known as “beach ridges,” plays a fundamental role in regional hydrological regulation by absorbing and releasing rainwater through surface and subsurface flows, in addition to contributing to water filtration and nutrient and sediment retention. The streams studied originate within this environmental context, with predominantly sandy soils and a strong fluvial-estuarine influence. Although each watercourse follows an independent path, all ultimately drain, directly or indirectly, into Patos Lagoon. The three streams share geomorphological characteristics typical of the southern Brazilian coastal plain, such as a meandering course, low gradient, predominantly sandy substrates, and origins in Holocene wetlands (Sfredo & Tagliani 2016), although they differ in their conservation status and landscape

characteristics. The climate is humid subtropical (temperate climate with no dry season and hot summers), classified as Cfa according to the Köppen–Geiger system (Alvares et al. 2013), with higher temperatures in summer and lower temperatures in winter, a mean annual temperature of 19.0 °C, and relatively well-distributed precipitation throughout the year, with a mean annual total of 1,366.45 mm (Reboita & Kruche 2018).

The Bolaxa Stream (32°09'46.6"S, 52°11'15.0"W) represents the least urbanized environment within the gradient considered in this study and is of high regional importance due to its water volume (Batista et al. 2007) and the presence of riparian forest composed of several plant species (Dorneles et al. 2013). It is located within the Lagoa Verde Environmental Protection Area (EPA), where it constitutes one of the few relatively preserved remnants in the region (Ferretti 2020). The stream is crossed by the RS-734 highway, which represents a linear infrastructure element associated with the stream crossing. The Martins Stream (32°05'14"S, 52°12'01"W), representing the intermediate-urbanization environment, is located at the edge of the Carreiros neighborhood and occurs within a peri-urban context characterized by a mosaic of land uses, combining remnants of riparian vegetation, open areas associated with pastures, and recently urbanized areas. The stream is influenced by regional road infrastructure, particularly the BR-392 highway, and lies within a land-use matrix intermediate between predominantly natural and urban environments.

The Cabeças Stream (32°04'37"S, 52°15'16"W), representing the most urbanized environment, is located in the Vila da Quinta community and occurs within an urban setting that has undergone a history of structural modifications associated with human occupation. The channel has low sinuosity, straight sections, and sectors with partial channelization, in addition to a substantial reduction in riparian vegetation along its course and strong influence from surrounding impervious surfaces.

Characterization of the sample areas

To complement the characterization of the study areas, aerial imagery was obtained using an unmanned aerial vehicle (UAV), model DJI Mini 3 Pro, on April 3, 2025. The images allowed the landscape and morphology of the fluvial systems to be documented and analyzed at high spatial resolution, providing a standardized basis for characterizing the sampled environments. The flights covered the entire extent of the transects surveyed on foot.

For land-use and land-cover classification, only orthomosaic images were used to ensure continuous coverage of the study area. Processing was performed in QGIS (version 3.34.6) integrated with the Orfeo ToolBox (OTB). Initially, the bank lines of each stream were digitized. Based on these lines, a 20-m-wide buffer was

established on both sides, resulting in a 10-m strip extending toward the stream channel and a 10-m strip extending into the adjacent terrestrial area. This strip, corresponding to the first 10 m from each stream bank, delimited the area of interest for the analysis.

A supervised classification approach was adopted. First, image segmentation was performed to generate vector objects based on spectral similarity. Three final land-use and land-cover classes were then defined: marginal terrestrial vegetation, sandbanks, and urbanized areas. The classifier used was an Artificial Neural Network (ANN), based on the RGB bands of the images — corresponding to the red, green, and blue channels (Barros et al. 2020). The “marginal terrestrial vegetation” class included all terrestrial vegetation cover present within the buffer zone surrounding the streams (10 m from each stream bank), regardless of floristic composition or successional origin. After automatic classification, a detailed manual review and correction of the vector layer were performed to correct algorithm inconsistencies, particularly in shaded areas.

Biological data collection

Data collection was conducted monthly from August 2024 to July 2025 along a sampling transects established in each of the Cabeças, Martins, and Bolaxa streams, always along the same bank at each site to standardize the sampling route. The distance effectively surveyed varied among campaigns due to field conditions, such as flooding, water level, substrate conditions, vegetation, and changes in the bank conditions. Surveyed transect lengths per campaign ranged from 602 to 864 m in CabStr, from 722 to 797 m in MarStr, and from 759 to 829 m in BolStr. Sampling prioritized non-invasive techniques, focusing on the identification of direct and indirect signs of the Neotropical otter, including feces, footprints, scratches, latrines, dens, and resting areas. Resting areas were defined as locations characterized by shallow depressions in the substrate, generally associated with disturbed and compacted sediment, frequently accompanied by footprints, scratches, or other recent signs of species presence. This type of approach has been widely adopted by several authors studying semiaquatic mammals (Kasper et al. 2004; Perinchery et al. 2011; Rheingantz et al. 2017), particularly to avoid interfering with the behavior of the monitored species.

During surveys, the stretches were traversed on foot, always using the eastern bank of the three streams. To minimize false positives and ensure taxonomic reliability, only signs displaying clear and unambiguous diagnostic features of the species were recorded. For feces, the criteria considered were characteristic odor and the presence of prey remains (scales, carapaces, hair, and feathers) deposited at sites near to the water were considered; for footprints, the diagnostic pattern of five digits and the presence of interdigital webbing were

assessed; and scratch marks associated with sandy substrates along stream banks were also recorded. In cases of uncertainty, identification was cross-checked against field identification guides (Prist et al. 2020); when uncertainty regarding the origin of the sign persisted, the record was excluded from the analyses. To minimize the risk of double-counting fixed signs, particularly scratch marks on sandy banks, a field marking procedure was adopted, consisting of discreet horizontal mark placed over previously recorded signs.

For each identified sign, the type, geographic coordinates (recorded using a handheld GPS device), field observations, and photographs were recorded. Fecal samples were collected and stored in individual sterile zip-lock bags, following the protocols described by Trinca et al. (2013) and Rheingantz et al. (2017). After collection, samples were kept frozen until analysis. Food items were identified through visual inspection of undigested fragments after washing the samples, following the method used by Colares & Waldemarin (2000). The main food groups (fish, crustaceans, insects, birds, amphibians, and others) were recorded for each sample. Identification was performed using broad trophic categories because the food items were too fragmented to allow more precise taxonomic identification. In addition, complementary environmental observations were made, including the presence of domestic animals, accumulated solid waste, human presence along the stream banks, and sewage discharge, in order to assist in the interpretation of the results.

Data analysis

Records of Neotropical otter signs were organized by stream and by monthly sampling campaign and standardized according for sampling effort. Although sampling was conducted monthly, monthly encounter-rate data were pooled into four seasons (summer, autumn, winter, and spring) to visualize temporal patterns. Statistical analyses of temporal variation were performed using the monthly data. For each sampled stream, the encounter rate was calculated as the total number of signs divided by surveyed distance (in kilometers) (signs/km).

To assess potential differences in sign encounter rates among streams and across seasons, the data were tested for compliance with the assumptions of parametric analyses using the Shapiro–Wilk test (normality of residuals) and Levene’s test (homogeneity of variances). The assumption of normality was violated, and Levene’s test indicated heterogeneity of variances. Therefore, a non-parametric Kruskal–Wallis test was used. When significant differences were detected, Dunn’s post hoc for multiple comparisons, with Bonferroni correction, was applied.

For diet, the following metrics were calculated for each food item: frequency of occurrence (FO), which expresses the proportion of samples in which a given item was present, and relative frequency of occurrence (FOR%), which represents the proportional contribution of each item relative to the total number of food-item records across all samples. These metrics describe patterns of occurrence and relative frequency of food items and do not directly reflect dietary biomass or energetic content. This approach is commonly used in studies of otter diet (Putman 1984; Kruuk 2006; Leite et al. 2007; Quintela & Colares 2008; Quintela et al. 2012; Sousa et al. 2013).

Similarly, diet composition was analyzed using a presence–absence matrix of food categories (fish, crustaceans, and birds) for each fecal sample. To assess differences in diet composition among streams and seasons, a permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarity was performed with 999 permutations, testing the factors site (i.e., streams) and season, and their interaction, using the *adonis2* function of the *vegan* package (Oksanen et al. 2024).

Additionally, patterns of similarity in diet composition were explored using non-metric multidimensional scaling (NMDS), also based on Bray–Curtis dissimilarities, with two dimensions ($k = 2$). The goodness of the ordination fit was assessed using the stress value, with lower values indicating a better representation of the underlying data structure. The NMDS ordination was used exclusively as an exploratory and visual tool, without inferential purposes, complementing the PERMANOVA results.

All statistical analyses and data visualizations were performed in the R environment (version 4.4.1; R Core Team 2025). Database organization and standardization were performed using functions from the *janitor* package (Firke 2023) and data-manipulation function from the *dplyr* (Wickham et al. 2023) and *tidyr* (Wickham et al. 2024) packages, as along with temporal-variable processing using *lubridate* (Grolemund & Wickham 2011). All graphical outputs in the manuscript, including boxplots of sign distribution, the two-dimensional NMDS ordination, and comparative bar charts of land-cover and riparian-vegetation percentages, were generated using the *ggplot2* package (Wickham 2016). General location maps and the spatial distribution of sign sampling points were produced using QGIS (QGIS Development Team 2024).

Results

Supervised characterization of sampled areas

Supervised classification of the riparian zone revealed structural differences among the three environments along the urbanization gradient (Fig. 2). In the most urbanized environment, marginal terrestrial vegetation covered 80.87% of the area. Although it was the dominant class, this environment exhibited the highest anthropogenic pressure among the monitored sites, with the urbanization class accounting for 16.08% of the monitored stretch, including roads, buildings, and compacted soil directly affecting the marginal zone. Sandbanks accounted for 3.05% and occurred sparsely, indicating localized areas of sediment deposition. In the intermediate-urbanization environment, marginal terrestrial vegetation covered 91.85% of the area. Unlike in the most urbanized environment, urbanized areas were limited (4.74%), being restricted to localized access points such as the BR-392 highway. Active fluvial dynamics were evident, with sandbanks present along 3.40% of the monitored stretch. Finally, in the least urbanized environment, marginal terrestrial vegetation reached its highest extent, covering 97.34% of the monitored stretch, while urbanization was minimal, accounting for only 2.66% of the monitored area.

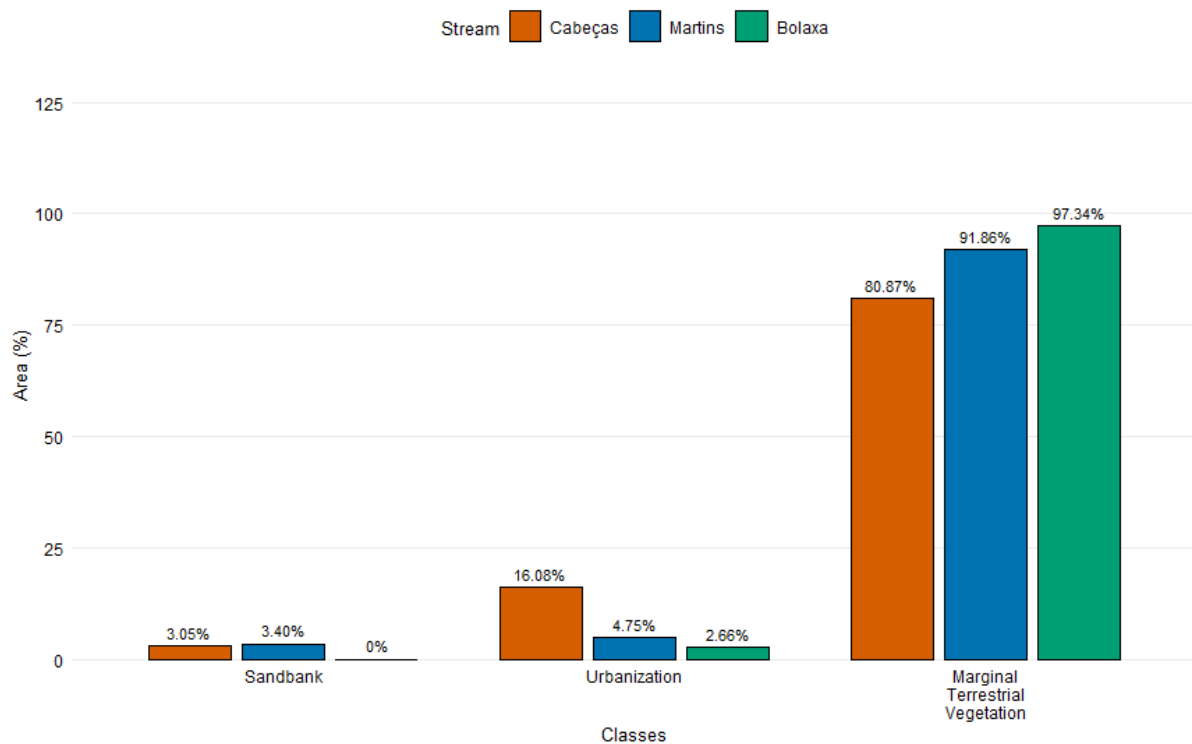


Fig. 2 Percentage distribution of land-use and land-cover classes within the 10-m buffer of environments classified according to the urbanization gradient: most urbanized, intermediate urbanization, and least urbanized. The classes include sandbank, urbanization, and marginal terrestrial vegetation. A conservation gradient can be observed, with a progressive increase in marginal terrestrial vegetation cover and a reduction in urbanization from the most

urbanized toward the least urbanized environment, indicating differences in the structural integrity of riparian habitat among the systems analyzed

Signs

A total of 175 occurrences of Neotropical otter signs were recorded, including 133 in the intermediate-urbanization stream, 29 in the most urbanized stream, and 13 in the least urbanized stream.

In total, 122 georeferenced occurrence points of Neotropical otter signs were recorded along the sampled streams. Sandbanks were the microhabitats most frequently associated with signs, accounting for 116 occurrences (95.1%). Vegetation was associated with three occurrences (2.5%), whereas concrete structures and fallen trunks accounted for two (1.6%) and one occurrence (0.8%), respectively (Table 1). When analyzed by stream, all points recorded in the stream within the intermediate-urbanization landscape occurred on sandbanks (100%). In the most urbanized stream, 23 of the 24 points (95.8%) were likewise recorded in this microhabitat, with only one record (4.2%) associated with vegetation. In contrast, the least urbanized stream exhibited greater heterogeneity in microhabitat use, with occurrences distributed among sandbanks (44.4%), vegetation (22.2%), concrete structures (22.2%), and fallen trunks (11.1%).

Table 1 Distribution of georeferenced Neotropical otter occurrence points among the different microhabitats recorded during the study period. Each coordinate point was considered a single sampling unit, regardless of the number of signs observed at the location

Stream	Sandbank	Vegetation	Concrete	Trunk	Total
Cabeças	23 (95.8%)	1 (4.2%)	0 (0%)	0 (0%)	24 (19.7%)
Martins	89 (100%)	0 (0%)	0 (0%)	0 (0%)	89 (73.0%)
Bolaxa	4 (44.4%)	2 (22.2%)	2 (22.2%)	1 (11.1%)	9 (7.4%)
Total	116 (95.1%)	3 (2.5%)	2 (1.6%)	1 (0.8%)	122 (100%)

Habitat use and seasonality

The intermediate-urbanization stream had the highest sign encounter rate, with 14.3 signs/km, followed by the most urbanized stream, at 3.60 signs/km, and the least urbanized stream, at 1.35 signs/km.

The streams differed significantly in sign encounter rate (Kruskal–Wallis test: $H(2) = 24.60$; $p < 0.001$). Dunn’s post hoc test confirmed that the intermediate-urbanization stream had significantly higher encounter rates than both the most urbanized stream ($p = 0.0017$) and the least urbanized stream ($p < 0.001$), whereas the latter two did not differ significantly from each other ($p = 0.515$) (Fig. 3).

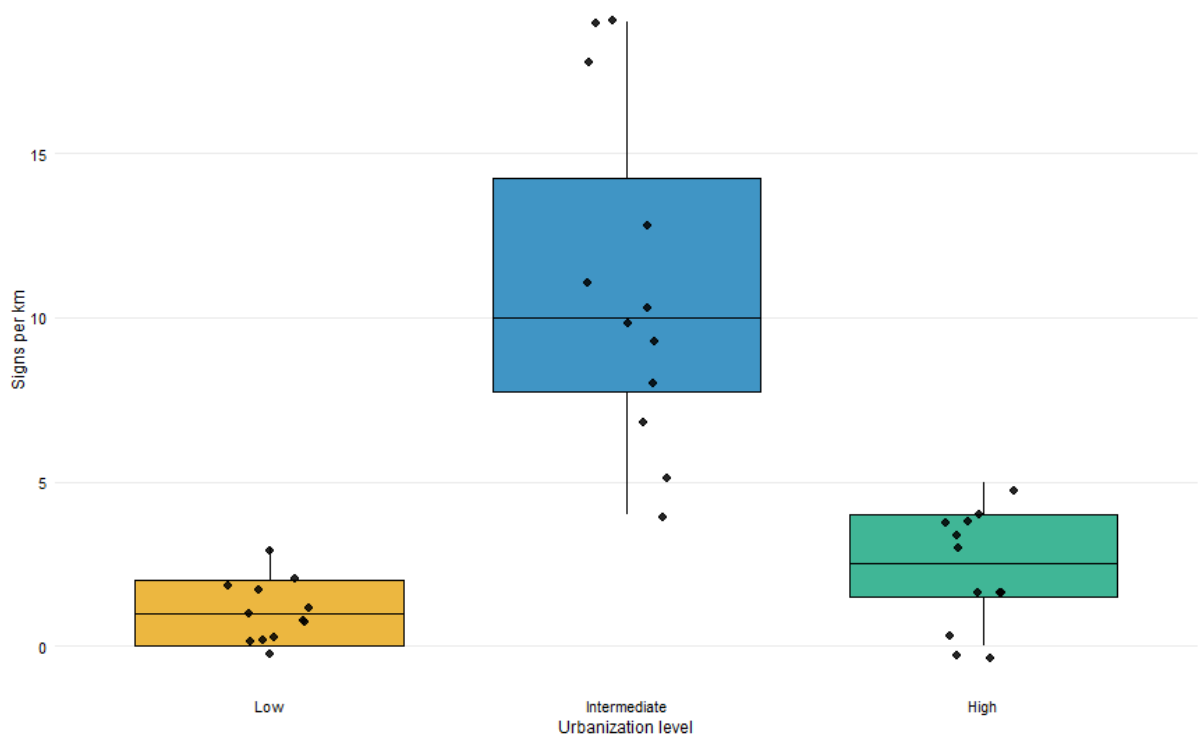


Fig. 3 Variation in the mean Neotropical otter sign encounter rate (signs/km) among the Bolaxa, Cabeças, and Martins streams

The analysis of monthly sign encounter rates showed no significant differences among sampled months ($H(11) = 2.30$; $p = 0.997$). For visualization, monthly values were grouped into four seasons (Fig. 4). Thus, no statistically significant seasonality in the use of stream banks by the Neotropical otter was detected during the study period.

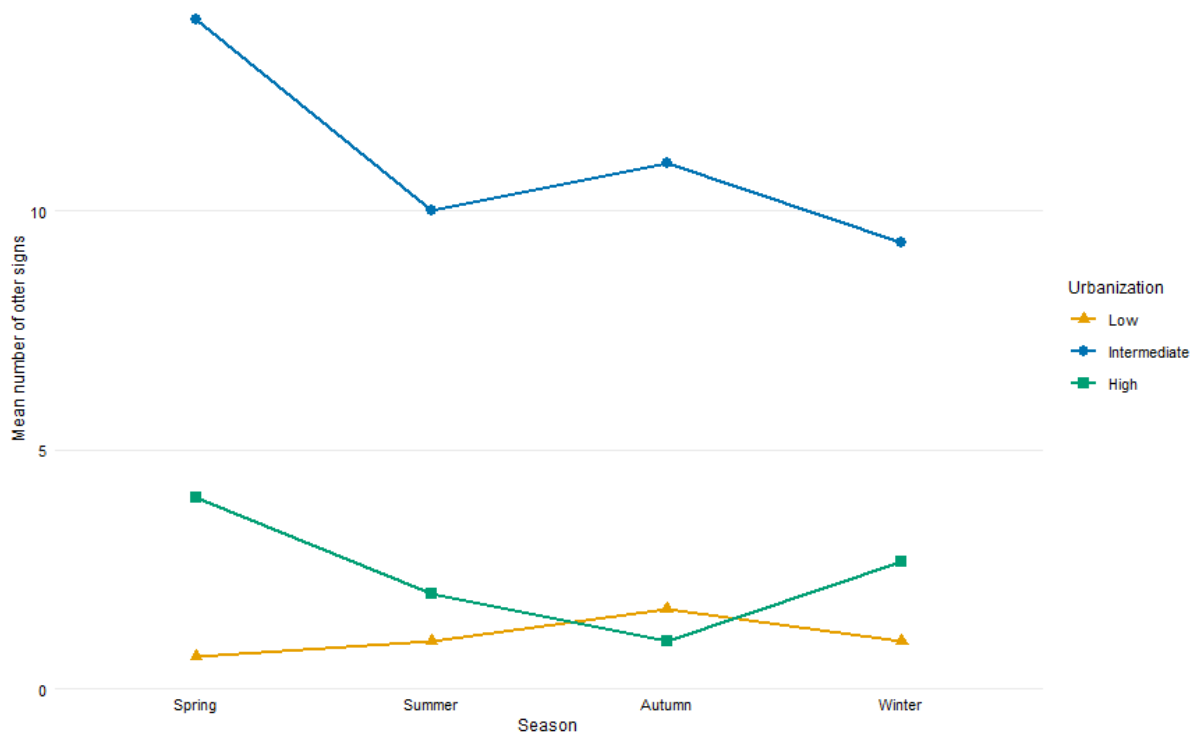


Fig. 4 Seasonal representation of sign encounter rates in each stream throughout the study period, based on monthly sampling data from August 2024 to July 2025

Landscape structure and encounter rate

Sign frequency did not follow the increase in marginal terrestrial vegetation cover among streams along the urbanization gradient. The least urbanized stream had the highest marginal terrestrial vegetation cover (97.34%) but the lowest sign encounter rate (1.35 signs/km). In contrast, the intermediate-urbanization stream had intermediate vegetation cover (91.85%) associated with the recurrent presence of sandbanks along the transect. Finally, the most urbanized stream had 80.87% vegetation cover and a rate of 3.60 signs/km.

Based on the heat maps, the most urbanized stream showed a relatively homogeneous distribution of signs, although the highest concentrations occurred at points farther from the urbanized area (Fig. 5). In contrast, the intermediate-urbanization stream exhibited a broad dispersion of signs throughout the sampled transect, with several high-intensity patches distributed along the bank. The least urbanized stream presented only isolated records, its banks predominantly occupied by grasses, with little exposed sandy substrates.



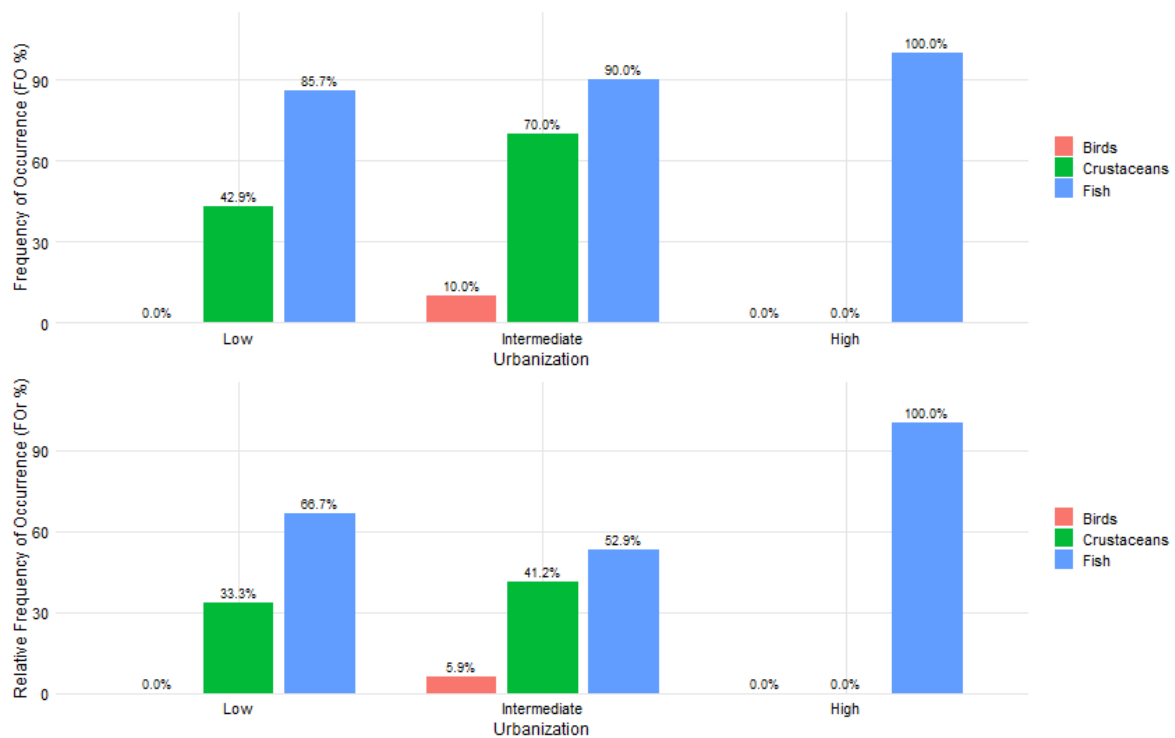
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287 **Fig. 5** Heat maps representing sign density in the Cabeças, Martins, and Bolaxa streams (August 2024 to July
288 2025)

289 Diet analysis

290 Diet composition differed among the streams studied. In the intermediate-urbanization stream ($N = 16$), fish
291 predominated ($FO = 87.5\%$; $FO_r = 58.3\%$), together with a substantial contribution of crustaceans ($FO = 56.2\%$;
292 $FO_r = 37.5\%$) and a single record of birds ($FO = 6.2\%$; $FO_r = 4.2\%$). In the least urbanized stream ($N = 10$), diet
293 exhibited a similarly fish-dominated pattern, characterized by strong dominance of piscivory ($FO = 90\%$; $FO_r =$
294 69.2%) and a moderate contribution from crustaceans ($FO = 40\%$; $FO_r = 30.8\%$). In the most urbanized stream

295 (N = 2), diet was more restricted, consisting exclusively of fish (FO = 100%; FOr = 100%) (Fig. 6).



296

297 **Fig. 6** Frequency of occurrence (FO%) and relative frequency of occurrence (FOr%) of food items recorded in
 298 *Lontra longicaudis* faeces from the Martins, Bolaxa, and Cabeças streams. The results indicate spatial differences
 299 in diet composition associated with environmental heterogeneity among the streams

300 The diet composition of the Neotropical otter exhibited descriptive fluctuations among seasons (Ntotal =
 301 28), although these fluctuations were without statistically significant variation (PERMANOVA: F = 1.99; p =
 302 0.168). Fish constituted the main food resource in all seasons, with the highest frequency of occurrence in winter
 303 (N = 5) and spring (N = 5) (FO = 100% in both), and similarly high values in autumn (N = 10) (FO = 80%) and
 304 summer (N = 8) (FO = 87.5%).

305 Despite the consistency of piscivory, its relative importance varied among seasons. In winter and spring,
 306 fish accounted for 83.33% of food occurrences (FOr). In summer and autumn, fish FOr decreased (to 53.8% and
 307 57.1%, respectively), concomitant with an increase in the contribution from crustaceans. Crustaceans showed their
 308 greatest representation during summer (FO = 75%; FOr = 46.1%) and autumn (FO = 50%; FOr = 35.7%), whereas
 309 in winter and spring, crustaceans had a smaller contribution (FO = 20%; FOr = 16.6%). Bird consumption was
 310 rare and restricted to autumn (FO = 10%; FOr = 7.1%) (Fig. 7).

311

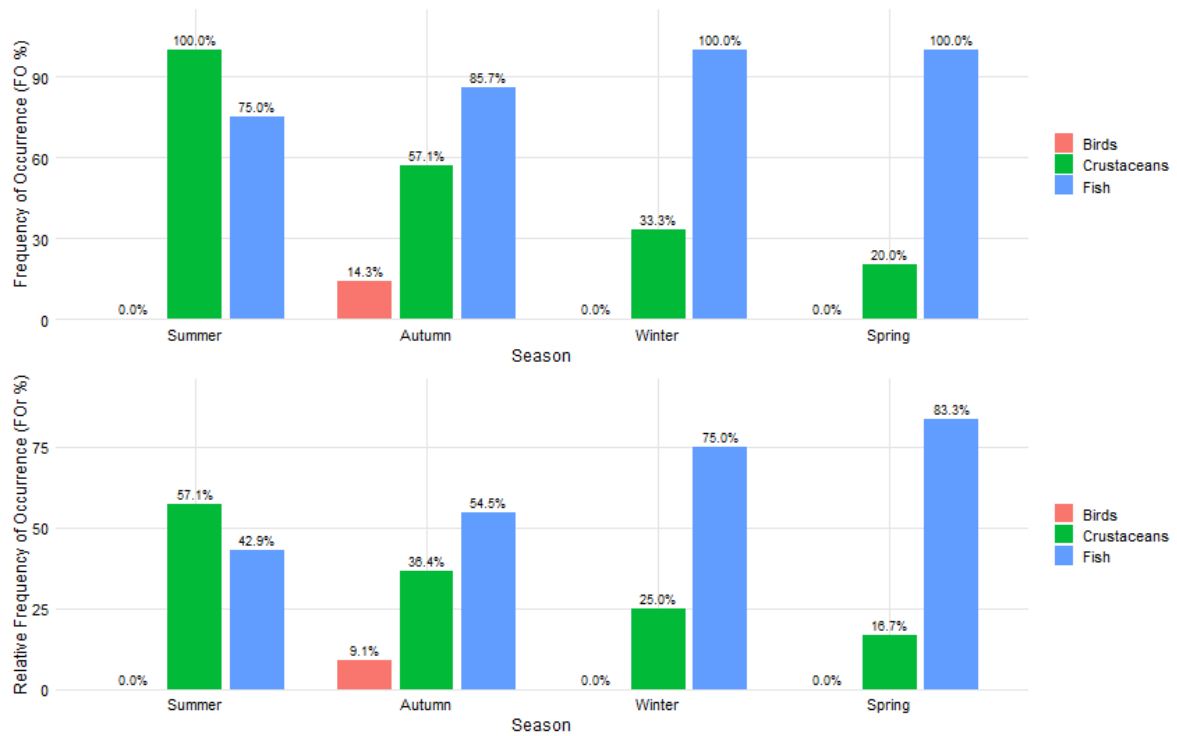


Fig. 7 Frequency of occurrence (FO%) and relative frequency of occurrence (FOR%) of food items identified in Neotropical otter feces, grouped by season. The bars represent percentage values for each food category, highlighting temporal variation in the occurrence and relative dominance of the resources used

No significant differences were observed in Neotropical otter diet composition for the stream $\times$ season interaction (PERMANOVA; $F = 0.51$; $p = 0.766$), or the stream factor alone ($F = 0.97$; $p = 0.425$) or for the season factor alone ($F = 1.99$; $p = 0.168$).

Consistent with the PERMANOVA result, the NMDS ordination yielded a very low stress value (stress = 0.026), indicating an excellent fit between the Bray–Curtis dissimilarities in the original matrix and the resulting two-dimensional representation. In ordination space, samples clustered relatively closely, reflecting the high consistency of piscivory in the diet, with considerable overlap among seasons and only slight visual differentiation, and not the formation of distinct clusters. The most urbanized environment occupied a more restricted position in multivariate space, apparently associated exclusively with fish consumption, but had low sampling representation (Fig. 8).

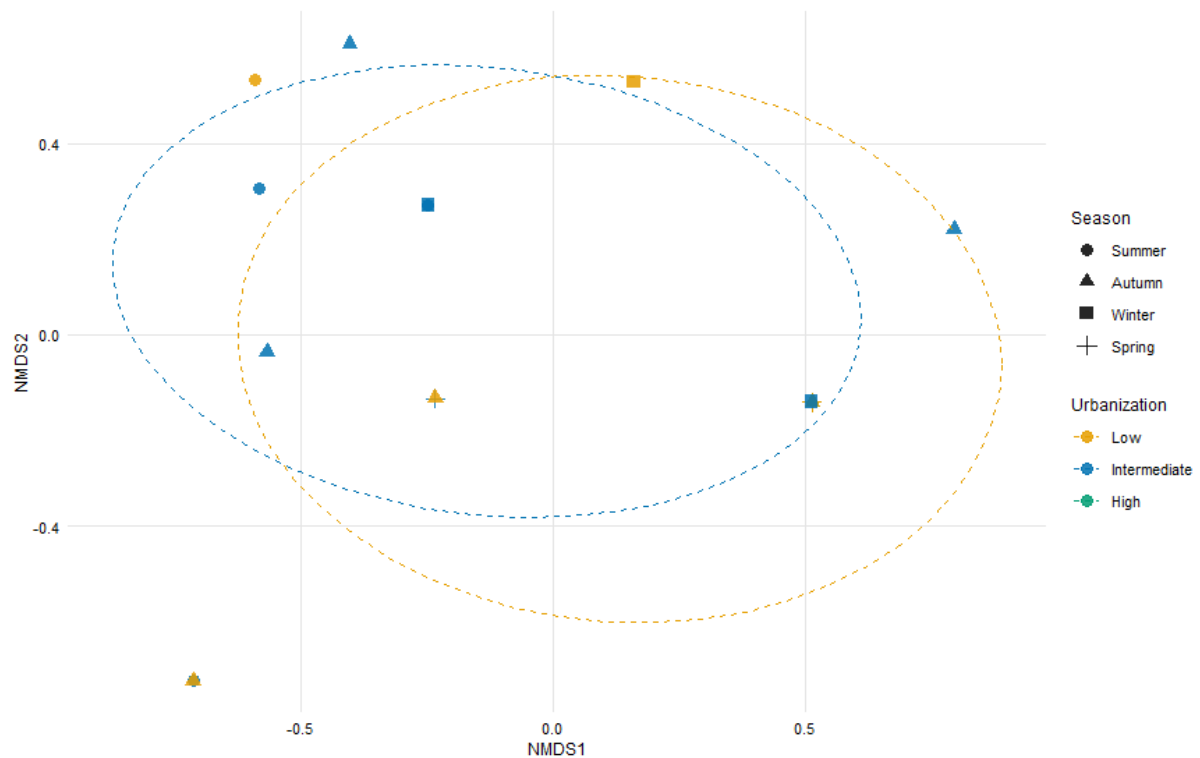


Fig. 8 Non-metric multidimensional scaling (NMDS) ordination of Neotropical otter diet composition, based on Bray–Curtis dissimilarities, using the presence of fish, crustacean, and bird categories in fecal samples. Points represent individual samples differentiated by season (symbols) and stream (colors). Ellipses indicate multivariate dispersion of samples by stream.

Discussion

Mapping of Neotropical otter signs revealed a pattern that diverged from expectations: sign presence did not track the gradient of marginal terrestrial vegetation preservation. The least urbanized environment, despite having the largest and most continuous vegetation strip (97.34% cover), showed the lowest sign encounter rate (1.35 signs/km). Conversely, the intermediate environment, although embedded within a peri-urban matrix, concentrated the highest number of records (14.3 signs/km). This pattern suggests that spatial-use intensity does not depend exclusively on vegetation cover and may instead be linked to the physical structure of the environment and to sign detectability. This interpretation is supported by the microhabitat analysis, in which approximately 95% of records occurred on sandbanks, indicating that the broad availability of this substrate influences both sign persistence and the resulting spatial pattern. In other words, record frequency likely reflects a combination of habitat use and detection probability, given that sandbanks are frequently used for movement, resting, and/or territorial marking.

In the least urbanized environment, the low encounter rate warrants cautious interpretation. This finding is consistent with Massara et al. (2026), who found no effect of natural riparian cover on Neotropical otter occupancy or detection probability across sections of the Paraopeba River, and instead reported higher record frequencies in sections with greater sandbank availability suggesting that fine-scale habitat structure and sign detectability strongly shape observed patterns. Accordingly, the high vegetation cover recorded in the least urbanized stream should not, in isolation, be interpreted as an indicator of greater use intensity by the species. Notably, this stream lies within a continuous network of wetlands, lagoons, and channels comprising the Lagoa Verde Environmental Protection Area (APA), rather than functioning as an isolated system. This connectivity may allow the otter to move among sections of the aquatic system, accessing feeding, shelter, and marking areas; consequently, even though local factors—such as proximity to the RS-734 highway and the presence of domestic animals—may reduce bank use and sign detectability, the system may remain functional as part of the species' broader movement network. As noted by Gu and Swihart (2004), failure to detect a species where it should occur is rarely random and often reflects systematic bias that distorts inferences about habitat–animal relationships, particularly where the environment conceals physical evidence. Here, the dominance of dense grasses (*Paspalum* spp.) along the banks may reduce footprint retention and other sign persistence, hindering field detection. This interpretation is further supported by the distribution of microhabitats in this stream, where records were spread among sandbanks, fallen trunks, concrete structures, and vegetated sections, without the strong predominance of a single microhabitat type observed elsewhere. Because sandbanks are deformable substrates, they retain footprints, scratches, and faeces, whereas the other microhabitats preserved only fecal records, lacking the physical conditions needed to retain other sign types.

The stream characterized as intermediate urbanized, despite being embedded within a peri-urban matrix, concentrated a markedly higher record density (14.3 signs/km). Aerial imagery revealed high hydromorphological complexity, with frequently exposed sandbanks (3.40% of the mapped area) and eroded banks. Although sandbanks represented only 3.40% of the area mapped within the 10-m bank buffer, they were distributed along multiple stream sections and occupied precisely the bank–channel interface—a zone potentially used more intensively for movement and territorial marking. Microhabitat results followed the same pattern: all records in this stream occurred on sandbanks. This suggests that record frequency here relates more closely to the spatial distribution of these substrates along the channel than to their overall proportional area, favoring both site use and sign persistence and thereby increasing detection probability relative to vegetated substrates. In terms of resource-use flexibility, this pattern parallels the opportunistic foraging behavior described for the North American river

otter (*Lontra canadensis*), whose diet varies with prey availability; in that system, habitat type appears to act as an initial filter on prey selection, while prey abundance, agility, and life-history traits act as secondary factors (Day et al. 2015). Although that study addresses a different species and a different aspect of resource use, its findings offer comparative support for the idea that environmental structure can mediate resource use independently of a direct, linear response to vegetation cover. Heat maps reinforce this interpretation, showing a more dispersed spatial distribution of signs throughout the intermediate stream, consistent with sandbanks occurring across multiple channel segments rather than being concentrated in a single sector. The near-total predominance of sandbank records also indicates that the efficiency of sign-based monitoring may depend strongly on the availability of this substrate; comparisons among streams should therefore consider not only the number of recorded signs, but also the spatial distribution of microhabitats capable of preserving them over time.

The most urbanized stream illustrates the effects of structural densification (16.08% urbanization). The lower mean encounter rate (3.60 signs/km), together with channel straightening, the presence of houses and streets, frequent vehicle and pedestrian traffic, and reduced marginal vegetation, reflects characteristics typically associated with urban stream degradation (Walsh et al. 2005), whereby physical channel simplification and intensifying pressures from the urban matrix alter system structure and function. Beyond these physical alterations, resident activity, domestic-animal presence, and other disturbance sources may influence otter behavior, reducing use of more exposed banks—consistent with Kerley et al. (2002), who showed that human disturbance can alter the behavior and performance of carnivorous mammals. As discussed by Yasué (2005), anthropogenic pressure creates a complex trade-off in which high local resource availability may lead animals to tolerate some disturbance, even though this coexistence imposes direct costs on foraging efficiency and optimal space use. Notably, the spatial distribution of signs within this stream shows that urbanization does not act homogeneously: the highest recorded concentration occurred in the relatively less urbanized sector of the sampled transect, indicating that even within a predominantly urban watercourse, locally less altered sectors can offer more favorable conditions for otter use. This underscores the importance of distinguishing average environmental conditions from the local-scale availability of refuges and favorable structures. The species' presence in this stream therefore does not necessarily indicate broad tolerance to urbanization but may instead reflect selective use of sectors retaining more favorable structural conditions. Recent findings for the marine otter, or chungungo (*Lontra felina*), along the Tarapacá coast of northern Chile similarly show abrupt declines where human overlap occurs, even in relatively well-preserved habitat (Pavez et al. 2026); although this involves a different species and a marine coastal system, it offers complementary evidence that otter responses to human presence may depend on

disturbance intensity and spatial distribution rather than habitat quality alone. Despite this scenario, nearly all records in the most urbanized stream also occurred on sandbanks, indicating that the pattern of microhabitat use remained consistent with that of the intermediate stream. Overall, differences in encounter rates across the urbanization gradient appear to stem mainly from structural changes in the system, the availability and distribution of substrates favorable for sign persistence, and disturbance intensity—rather than from clear shifts in microhabitat selection by the species itself.

Regarding temporal patterns, the absence of significant monthly variation in sign encounter rate suggests no strong seasonal pattern in bank use during the sampling period. This is consistent with regional literature on *Lontra longicaudis*, which reports relatively continuous use of aquatic environments in southern Brazil, albeit with variation in site-specific use intensity, sign detectability, and resource availability over time. In the Taquari Valley (Rio Grande do Sul), Kasper et al. (2008) documented recurrent, year-round use of shelters and latrines. Also in southern Brazil, Carvalho-Junior et al. (2010), studying Lagoa da Conceição on Santa Catarina Island (Florianópolis), found temporal variation in diet composition rather than in site persistence, suggesting an opportunistic response to fluctuations in prey availability. Within the Lagoa Verde APA itself, monthly monitoring of the Bolaxa Stream between July 2008 and June 2009 documented latrine reuse and continuous shelter use, reinforcing the species' spatial persistence in the region (Quintela et al. 2011). The consistency of sandbank records observed in the present study aligns with this regional pattern of continuous habitat use—although this stability should not be read as an absolute absence of temporal variation, since hydrology, resource availability, and sign detectability can all affect record frequency without necessarily reflecting changes in area occupancy.

Analysis of diet composition revealed a marked predominance of piscivory as the primary trophic strategy, complemented by crustacean and, occasionally, bird consumption. Although local variation in the frequency of occurrence of food items was observed, multivariate analyses (PERMANOVA and NMDS) detected no statistically significant differences in diet composition among urbanization levels, seasons, or their interaction. The intermediate stream exhibited the most diverse dietary pattern among the three environments. Although fish dominated (FO = 87.5%), the substantial contribution of crustaceans (56.25%) and the occurrence of birds (6.25%) reflect an opportunistic foraging strategy consistent with the trophic flexibility described for the species (Rheingantz et al. 2017). This dietary diversity may relate to the greater environmental heterogeneity of this stream, characterized by frequent aquatic vegetation, sandbanks, and varied microhabitats along the channel—

structural heterogeneity known to provide shelter and recruitment areas for juvenile fish and invertebrates, particularly crustaceans (Thomaz & Cunha 2010), potentially increasing their local availability and, consequently, their frequency in fecal samples. The least urbanized stream showed an intermediate diet-diversity pattern, with fish predominance (FO = 90%) accompanied by a moderate crustacean contribution (FO = 40%). Although this stream had the lowest sign encounter rate along the gradient, its diet composition indicates access to varied food resources. Previous studies have also highlighted the ecological importance of this stream for regional biodiversity conservation, documenting high species richness and its role as an ecological corridor within the municipality's coastal landscape (Batista et al. 2007; Dorneles et al. 2013). The low record frequency observed here should therefore not be read as evidence of poor environmental quality, but more plausibly as reflecting an interaction between detectability limitations and local factors influencing bank use and marking behavior. Finally, in the most urbanized stream, embedded within a matrix with 16.08% urbanization, diet was more restricted and composed exclusively of fish (FO = 100%). This result should nonetheless be interpreted cautiously, given the small number of fecal samples obtained from this stream (N = 2), which limits inferences about local dietary specialization.

Seasonal analysis showed that fish remained the primary food resource throughout the year. Although their frequency of occurrence stayed high across all seasons, crustaceans made a relatively greater contribution during summer and autumn, an opportunistic adjustment in resource exploitation that did not alter the overall piscivorous pattern. Bird consumption was rare and restricted to autumn, indicating an occasional dietary component. This combination of sustained piscivory with discrete seasonal fluctuations in secondary prey is well supported by regional literature: Kasper et al. (2004), in the Forquetinha Stream and Forqueta River (Taquari Valley, central Rio Grande do Sul), and Quintela et al. (2008), in the Bolaxa Stream, similarly reported fish as the year-round trophic base, with macrocrustaceans and small terrestrial or shallow-water vertebrates incorporated opportunistically as secondary prey, often coinciding with periods of low water level or local abundance peaks of these organisms.

The absence of significant differences in diet composition detected by PERMANOVA likely reflects the high trophic plasticity of the Neotropical otter, a species known to preferentially exploit the most abundant and energetically accessible resources available in each environment. Small local variations in prey availability thus tend to shift the frequency of particular food items without altering the overall, predominantly piscivorous, diet structure. This plasticity within an essentially piscivorous framework mirrors patterns described by Rheingantz et al. (2017) at the Neotropical scale and by Quadros and Monteiro-Filho (2001) in the Atlantic Forest, both showing

that the species adjusts prey proportions without destabilizing its core trophic niche. The urbanization levels represented in this study therefore do not appear sufficiently heterogeneous to significantly alter diet composition in the region, and the fish predominance observed across all environments follows a pattern widely documented for the subfamily Lutrinae (Larivière 1999; Medina-Vogel et al. 2003; Kruuk 2006). Local differences in environmental structure thus appear to influence the relative frequency of specific food items more than they reshape the species' overall, essentially piscivorous, trophic pattern.

Taken together, the results suggest that habitat use reflects a balance between resource availability, spatial or trophic, and survival risk. As proposed by Sih et al. (2011) and Rheingantz et al. (2017), risk perception and anthropogenic disturbance may be more determinant of species abundance and persistence than riparian vegetation cover alone. This is illustrated by the least urbanized stream, which shows a discrepant relationship between structural integrity and otter occurrence: despite lying within a protected area (EPA) and having the highest marginal vegetation cover in the sample (97.34%), it recorded the lowest sign encounter rate. This pattern is compatible with the concept of an ecological trap (Sih et al. 2011; Wong & Candolin 2015), whereby anthropogenic alteration decouples habitat-quality cues from the benefits organisms derive, leading them to select apparently favorable environments that impose greater survival risk or reduced fitness. Although the present data do not allow direct confirmation of this process, the stream's high structural quality may act as an attractant, while human-related factors may raise the costs of habitat use. The proximity of the RS-734 highway, associated traffic noise, and frequent human and domestic-dog presence may transform what would otherwise be a refuge into an environment of continuous disturbance (Yasué 2005). Under these conditions, otters may reduce use of certain stretches or limit exposure in more open areas—a behavior already documented in other otter species under high human presence, leading to underuse of apparently suitable habitat (Pavez et al. 2026). These risks are not merely theoretical: during this study, a road-killed individual was recorded, underscoring the species' vulnerability to regional road infrastructure. Risk is not limited to direct human impacts, either. The more frequent presence of domestic animals in the least and most urbanized streams raises concern regarding potential pathogen spillover, as indirect contact with dogs can expose native fauna to urban viruses and protozoans—threatening otter health even in areas without direct effluent discharge or within protected areas (Gonchoroski et al. 2025). Direct contact with free-ranging dogs also poses a threat through predation, persecution, and behavioral harassment, as these animals are recognized as significant threats to native mammals, acting as opportunistic predators and promoting spatial exclusion of sensitive species (Lessa et al. 2016). Together, these effects suggest an elevated cost of bank use for otters in anthropized streams, with potential consequences for their persistence and activity patterns and,

by extension, for the ecological functions the species provides, including prey control and seed/propagule dispersal (Hoffmann et al. 2025).

Conclusions

The investigation of Neotropical otter ecology in the streams of Rio Grande demonstrates that the persistence of this carnivore in coastal landscapes under anthropogenic influence is associated with the species high ecological plasticity. The results indicate that marginal terrestrial vegetation cover alone does not explain the observed patterns of habitat use. Sign intensity was associated with the interaction among different landscape components, including the availability of microhabitats capable of preserving signs, connectivity among aquatic environments, and the influence of anthropogenic disturbances. These results highlight the importance of jointly interpreting ecological factors and the limitations related to sign detectability. Similarly, diet remained predominantly piscivorous across the entire urbanization gradient, despite the differences observed in the frequency of occurrence of food items among the environments evaluated. This pattern corroborates findings widely described for the species and reinforces its high trophic plasticity. In addition, the absence of a detectable seasonal pattern in sign encounter rates suggests year-round use of the environments throughout the year, consistent with findings from studies conducted in southern Brazil. These results reinforce that Neotropical otter conservation depends on strategies extending beyond the simple maintenance of riparian vegetation. Preservation of functional connectivity among aquatic environments, mitigation of impacts associated with road infrastructure, appropriate management of domestic animals, and reduction of other sources of anthropogenic disturbance constitute priority actions for ensuring the persistence of the species in landscapes under increasing human influence. Finally, future studies should integrate complementary monitoring methods, such as camera traps, telemetry, and molecular techniques, to reduce limitations related to sign detectability and to improve understanding of spatial-use patterns, habitat selection, and species responses to different levels of environmental disturbance.

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677 **Competing Interests** The authors declare no competing interests.

678 **Ethics Approval and Consent to Participate** Not applicable. The study involved non-invasive observations and
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680 **Data Availability** The data that support the findings of this study are available from the corresponding author
681 upon reasonable request.

682 **Author Contributions** Alan Lopes: Conceptualization, Methodology, Investigation, Data Curation, Formal
683 Analysis, Visualization, Writing – Original Draft, Writing – Review & Editing. Fabiana Schneck:
684 Conceptualization, Methodology, Supervision, Writing – Review & Editing. Eduardo R. Secchi:
685 Conceptualization, Methodology, Supervision, Writing – Review & Editing.