



Lethal restaurant: The trophic ecology of a bird of prey in highway-fragmented landscapes

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ABSTRACT

Highways can alter the foraging behavior of top predators, such as raptors, by providing carcasses and attracting prey associated with human-modified environments or in areas preserved by set-aside areas along roads. However, exploiting these resources near roads increases the risk of collisions and poses additional conservation challenges. Here, we investigated the diet and individual specialization of Great Horned Owls (*Bubo virginianus*, $n = 26$) killed on highways in southern Brazil, integrating stomach content analysis with carbon and nitrogen stable isotope analysis (SIA) from multiple tissues. The species exhibited generalist feeding habits at the population level, with mammals (Prey-Specific Relative Importance Index, PSIRI% = 35.7) and insects (PSIRI% = 20.8) as the main prey items identified in stomach contents. SIA indicated a predominant assimilation of mammals in muscle (95% Credible Intervals CI = 20.4–48.2%), liver (95% CI = 25.9–58.4%), and feathers (95% CI = 30.7–60.2%), followed by amphibians (muscle: 95% CI = 3.5–38.9%; liver: 95% CI = 3.2–45.4%; feathers: 95% CI = 2.8–44.8%). Isotopic data also revealed high individual specialization, particularly reflected by carbon isotopic variation, suggesting consistent consumption of different prey groups or prey mixtures among individuals. Such specialization may lead to differential exposure to roadkill risk in anthropogenic landscapes, both by feeding on carcasses or preying in set-aside areas along roads. The integration of traditional dietary and isotopic approaches, unprecedented for this species, provides novel insights into the trophic ecology of the Great Horned Owl in highway-fragmented ecosystems of southern Brazil and underscores the importance of considering intraspecific variability in ecological and conservation studies.

1. Introduction

Animal foraging behavior can be strongly influenced by environmental changes, particularly those resulting from human activities such as the construction and expansion of highways. These infrastructures fragment habitats and alter the spatial distribution and abundance of food resources, either by providing carcasses of roadkilled animals or by attracting prey species associated with roadside vegetation (Allen and Taylor, 2013; Allen et al., 2019). However, exploiting these resources also increases the risk of mortality from vehicle collisions (Bernardino et al., 2020). Thus, a trade-off emerges between food availability and collision risk, which may vary according to each predator's foraging strategy and degree of dietary specialization (Votier et al., 2010).

Birds of prey play a key role in ecosystem functioning by regulating prey populations (Udrizar-Sauthier et al., 2017) and controlling synanthropic species such as rodents in human-modified environments

(Muñoz-Pedreros et al., 2010; Luna et al., 2020). Understanding the trophic ecology of raptors is therefore essential to elucidate their ecological roles as top predators (Petrovici et al., 2013; Romanowski and Lesiński, 2020) and to assess their vulnerability to anthropogenic threats, such as vehicle collisions leading to road mortality. This is particularly relevant in regions where extensive road networks intersect natural or semi-natural habitats, as occurs in southern Brazil, where highways traverse landscapes that include protected areas, increasing the exposure of wildlife to collisions.

To understand how such anthropogenic factors shape the trophic ecology of raptors, different methodological approaches can be combined, ranging from traditional stomach content analysis to stable isotope analysis (SIA). Stomach content analysis allows precise identification of undigested prey remains (Marti et al., 2007; Dove and Coddington, 2015), but relies on access to carcasses or museum specimens (Currie et al., 2003). Complementary methods such as SIA provide

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insights into food sources assimilated into tissues through the analysis of intrinsic isotopic markers, particularly carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) (Rubenstein and Hobson, 2004). Carbon isotopes reflect habitat use and basal carbon sources (Fry, 2006), while nitrogen isotopes indicate trophic position (Kelly, 2000). The analysis of tissues such as muscle, liver, or growing feathers enables evaluation of recent dietary assimilation due to their specific turnover rates (Rubenstein and Hobson, 2004). In raptors, SIA has been applied, for instance, to investigate sexual dietary segregation (Catry et al., 2016) and detect niche variation (Balza et al., 2020).

Although populations are often treated as ecologically homogeneous in dietary studies, individuals may exhibit substantial variation in resource use, a phenomenon known as intrapopulation niche variation (Bolnick et al., 2003). Such differences may result from ontogeny (Polis, 1984), sex (Shine, 1989), morphology (Smith and Skúlason, 1996), or from consistent individual specialization, independent of those factors (Bolnick et al., 2003). Populations with greater individual niche variation tend to show increased resilience to environmental changes (Sherratt and MacDougall, 1995), yet individuals adopting distinct foraging strategies may experience variable levels of risk exposure (Durell, 2000). Individual specialization is widespread across vertebrate taxa (e.g., Rossman et al., 2015; Bodey et al., 2018), including raptors such as the White-tailed Eagle (*Haliaeetus albicilla*) (Nadjafzadeh et al., 2016) and the Great Horned Owl (*Bubo virginianus*) (Duxbury and Holroyd, 1997). This variation in resource use can influence how species exploit roadside habitats and, consequently, their susceptibility to roadkill.

The Great Horned Owl is a large sized and widely distributed owl, found throughout the American Continent (Ostrow et al., 2023), known for its dietary flexibility encompassing mammals, birds, and invertebrates (Cisneros-Heredia et al., 2026). This nocturnal predator hunts often in open and fragmented landscapes, including areas influenced by highways (König and Weick, 2008). In southern Brazil, there is evidence that the species scavenges on roadkilled mammals (Anza and

Zilio, 2015), which may increase its exposure to vehicle collisions, a growing conservation concern (Bressan et al., 2009; Bodrati et al., 2017). Moreover, a recent record of predation on a young domestic cat further highlights its adaptability to urbanized landscapes, demonstrating its ability to exploit a wide range of environments and prey types (Cisneros-Heredia et al., 2026).

In this context, we investigated the trophic ecology of the Great Horned Owl in southern Brazil using a combination of stomach contents of road-killed owls and stable isotope analyses in tissues. By integrating these complementary methods we evaluated dietary composition and individual specialization within a population exposed to road-affected environments. We hypothesized that the species behaves as a generalist predator at the population level, but exhibits individual specialization linked to prey availability in different foraging habitats associated with highways. Therefore, most individuals are expected to exhibit a specialized diet (dominated by one or a few prey items), even when the population as a whole consumes a wide variety of prey.

2. Materials and methods

2.1. Study area

The state of Rio Grande do Sul (RS) is the southernmost of Brazil, bordering with Uruguay and Argentina, in South America, and encompasses two distinct biomes: the Pampa grasslands and the Atlantic Forest (Fig. 1). In coastal plains of the RS state, both biomes include extensive wetland systems such as marshes, lakes, and lagoons that sustain a rich diversity of fauna and flora (Denny, 1994). However, these ecosystems have been increasingly affected by anthropogenic disturbances, including highways that intersect protected areas (e.g., BR-471 crossing the Taim Ecological Station in the Pampa; Novelli et al., 1988) and large-scale monocultures, particularly irrigated rice fields. Such activities contribute to the fragmentation and degradation of natural habitats, altering the ecological dynamics and connectivity across the landscape



Fig. 1. Map of the study area in the state of Rio Grande do Sul, southern Brazil, where Great Horned Owl (*Bubo virginianus*; $n = 26$) individuals were collected, indicating the two biomes: Pampa grasslands and Atlantic Forest.

(Overbeck et al., 2007; Coelho et al., 2008).

2.2. Sample collection

Twenty-six specimens of Great Horned Owl found dead along highways crossing the Pampa and the Atlantic Forest biomes were opportunistically collected between the years 2000 and 2017. All samples were deposited in two scientific collections: the Bird Collection of the Federal University of Rio Grande (CAFURG) at the Subtropical Biodiversity Center (CBS) and the Museum of Science and Technology (MCP) of the Pontifical Catholic University of Rio Grande do Sul (PUCRS) (Table S1). During necropsy procedures, growing feathers ($n = 16$ birds), identified by the presence of vascularized calamus and/or a keratin sheath, muscle ($n = 12$), liver ($n = 12$), and stomach contents ($n = 23$) were sampled (Table S1). Feathers were stored in sterile plastic bags, while muscle and liver samples were individually frozen in Eppendorf tubes. Stomachs were preserved in 70% ethanol until analysis.

2.3. Stomach content analysis

Each stomach content was washed with running water through a 500 μm mesh sieve to separate food remains. Prey items were identified to the lowest possible taxonomic level under a stereomicroscope, with the assistance of taxonomic experts familiar with the regional fauna (see Acknowledgements). Identification was based on morphological keys and comparisons with specimens from the reference collections of the Federal University of Rio Grande - FURG. The numerical abundance of each prey category was determined by counting diagnostic structures such as skulls, mandibles, femurs, elytra, and exoskeleton fragments, thereby estimating the minimum number of individuals consumed. Unidentified fragments lacking diagnostic characteristics were grouped into broader taxonomic categories to ensure consistency in prey classification.

Prey body mass was estimated using data from the laboratory's reference database, which contains morphometric and weight information for potential prey species occurring in the study area. For partially digested prey, mass was inferred by comparison with individuals of similar size in the database, while intact prey items were weighed directly when possible.

2.4. Stable isotopes analysis (SIA)

Samples of liver, muscle, and growing feathers were collected from Great Horned Owls because these tissues integrate dietary information over relatively recent and complementary temporal windows, ranging from a few days to a few weeks, respectively (Inger and Bearhop, 2008; Boecklen et al., 2011). All tissues, as well as muscle tissue from prey items found in their stomachs, were analyzed for stable carbon and nitrogen isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Lipid extraction was performed on liver and muscle samples from owls, and on muscle from prey items, to prevent lipid interference with $\delta^{13}\text{C}$ values (Schlechtriem et al., 2003). The extraction consisted of three 8-h cycles in a Soxhlet apparatus using a chloroform:methanol solution (1:2). Growing feathers were cleaned to remove external contaminants by washing in shaking tubes with a sodium hydroxide (NaOH) solution, followed by distilled water rinsing, according to standard laboratory protocols. Feathers were then oven-dried at 70 °C for 12 h, cut into small fragments, and the rachis was excluded from analysis. All samples were homogenized, and approximately 0.7 mg of each was weighed into tin capsules for measurement using an isotope ratio mass spectrometer (IRMS) coupled to an elemental analyzer, at the Stable Isotope Center, University of New Mexico (UNM), USA. Isotopic composition was expressed in delta (δ) notation, in parts per thousand (‰), representing the deviation of the sample's isotopic ratio (R) relative to international standards, Vienna Pee Dee Belemnite (VPDB) for carbon, and atmospheric air for nitrogen,

according to Bond and Hobson (2012):

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} (\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \quad (1)$$

2.5. Data analysis

To describe the diet of Great Horned Owls, the relative frequency of occurrence (%FO), the relative contribution by number (%N), and the relative contribution by mass (%M) of each prey item identified in stomach contents were calculated. Prey-specific contributions were also calculated following Brown et al. (2012), including the mean contribution by number (%PN) and mass (%PM), which is based only on stomachs in which a given prey item occurred. The %PN and %PM values, together with %FO, were used to calculate the Prey-Specific Relative Importance Index (PSIRI%), as proposed by Brown et al. (2012):

$$\text{PSIRI}\% = [(\%PN + \%PM) * \%FO] / 2 \quad (2)$$

PSIRI% values provide information on the importance of prey species by relating their occurrence parameters to their estimated numerical and mass contributions (Brown et al., 2012). In this way, it is possible to balance the contribution of prey species without over-emphasizing those that contribute significantly in numerical terms but have a low frequency rate.

For SIA, a Bayesian stable isotope mixing model was built using the *Stable Isotope Mixing Models in R* (SIMMR) package (Parnell et al., 2013). The models included four groups of potential prey (insects, amphibians, birds, and mammals), selected based on the most important prey items identified in the stomach contents analysis (Table 1). Markov Chain Monte Carlo (MCMC) simulations were performed using the default SIMMR settings: four chains, 10,000 iterations, a burn-in of 1000

Table 1

Stable isotope values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) (mean $\pm$ SD) in tissues of potential prey used in the isotopic mixing models of Great Horned Owl (*Bubo virginianus*) tissues collected on highways in southern Brazil. Insect values are from Bosenbecker and Bugoni (2020), who sampled individuals from the same geographic area and during the same period as the owls included in this study. The values of other prey items were obtained from specimens found in the stomach contents of owls.

Taxon	Tissue sample	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Predator			
<i>Bubo virginianus</i>	Liver ($n = 12$)	-21.16 ± 1.80	12.22 ± 0.55
	Muscle ($n = 12$)	-21.38 ± 1.37	10.56 ± 0.54
	Growing feathers ($n = 16$)	-19.72 ± 1.77	13.22 ± 0.98
Potential food sources			
Invertebrates			
Insects	$n = 5$	-26.17 ± 0.84	4.66 ± 0.15
Lepidoptera (caterpillar)	Whole body ($n = 1$)	-25.6	4.5
Orthoptera	Whole body ($n = 1$)	-26.4	4.5
Orthoptera	Whole body ($n = 1$)	-26.6	4.8
Orthoptera	Whole body ($n = 1$)	-27.2	4.8
Coleoptera: Scarabaeidae	Whole body ($n = 1$)	-25.07	4.71
Vertebrates			
Amphibians	$n = 2$	-23.31 ± 3.5	9.73 ± 1.25
<i>Leptodactylus latrans</i>	Muscle ($n = 1$)	-20.83	10.62
<i>Leptodactylus latrans</i>	Muscle ($n = 1$)	-25.79	8.84
Mammals	$n = 2$	-17.97 ± 2.41	9.64 ± 0.14
<i>Holochilus vulpinus</i>	Muscle ($n = 1$)	-19.68	9.75
<i>Holochilus vulpinus</i>	Muscle ($n = 1$)	-16.26	9.54
Birds	$n = 2$	-24.7 ± 1.33	10.71 ± 0.52
<i>Myiopsitta monachus</i>	Muscle ($n = 1$)	-25.64	11.08
<i>Molothrus bonariensis</i>	Muscle ($n = 1$)	-23.76	10.34

iterations, and a thinning interval of 10. Because species-specific Trophic Discrimination Factors (TDFs) were unavailable for this species, mean values and standard deviations were estimated for each tissue type using the *Stable Isotope Discrimination Estimation in R* (SIDER) package (Healy et al., 2018). Additionally, the Mixing Polygon package (Smith et al., 2013) was used to visually assess the suitability of the estimated TDFs by verifying that the isotopic values of the consumer tissues were encompassed within the mixing polygon defined by the potential prey sources after TDF correction (Table S2). A correlation matrix of the estimated contributions of potential prey to each tissue was generated using the SIMMR package (Parnell et al., 2013) to evaluate the posterior correlations among prey sources in the Bayesian mixing models (Smith et al., 2013) (Fig. S1, S2 and S3).

To assess individual dietary specialization, only individuals with samples from all three tissues (growing feathers, liver, and muscle) were included ($n = 7$). The analysis was conducted using both uncorrected and TDF-corrected $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values, with TDFs applied to account for differences in isotopic discrimination among tissues. TDFs used were the same used in mixing models (Table S2). This procedure tries to avoid errors associated to metabolic routing for synthesis of distinct tissues. Both approaches, with corrections (e.g. Herrera et al., 2006) and without corrections (e.g. Martínez del Río et al., 2009; Petit et al., 2023), had been used. The Total Niche Width (TNW), representing the full range of prey consumed by the population, was partitioned into two components: the Within-Individual Component (WIC), reflecting diet variation within individuals, and the Between-Individual Component (BIC), corresponding to dietary variation among individuals. The WIC/TNW ratio was calculated using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from individual owls with multiple tissues representing different time-windows, and thus the total isotopic variance partitioned into WIC and BIC (Vander Zanden et al., 2013). The analysis was conducted based on ANOVA-derived variance components, allowing estimation of dietary specialization at the individual level. Values approaching 0 indicate specialist individuals, while values closer to 1 indicate generalist individuals (Bolnick et al., 2003).

3. Results

3.1. Stomach content analysis

A total of 23 Great Horned Owl stomachs were analyzed, of which 17 contained prey remains. In total, 44 individual prey items were recorded, encompassing both invertebrates and vertebrates. The most frequent prey categories were insects (%FO = 76.4), small mammals (%FO = 52.9), and amphibians (%FO = 35.2) (Table 2). Rice grains (*Oryza sativa*, $n = 32$) were found in one stomach, likely resulting from secondary ingestion through a granivorous bird preyed upon by the owl.

According to the Prey-Specific Relative Importance Index (PSIRI%), small mammals represented the most important dietary component (PSIRI% = 35.7). Among them, the Marsh Rat *Holochilus vulpinus* was the most important prey species (PSIRI% = 14.4). Insects ranked second in importance (PSIRI% = 20.8), with water bugs (Belostomatidae; PSIRI% = 5.8) and crickets (Gryllidae; PSIRI% = 5.8) contributing equally to the diet. Amphibians also played a relevant role (PSIRI% = 19.0), particularly species of Leptodactylidae.

3.2. Stable isotopes analysis (SIA)

In muscle tissue, small mammals contributed most to isotopic composition (95% CI = 20.4–48.2%), followed by amphibians (95% CI = 3.5–38.9%) and birds (95% CI = 6.9–35.2%) (Fig. 2). A similar pattern was observed for liver (small mammals: 25.9–58.4%; amphibians: 3.2–45.4%; birds: 8.0–41.7%) (Fig. 3) and for growing feathers (small mammals: 30.7–60.2%; amphibians: 2.8–44.8%; birds: 8.7–43.8%) (Fig. 4). Invertebrates showed the lowest contribution to the diet across all tissues, with mean values below 20%. The analysis of individual

Table 2

Contribution of food items ($n = 44$ prey items counted, total mass = 1.766 kg) to the diet of the Great Horned Owl (*Bubo virginianus*) obtained through the analysis of stomach contents ($n = 17$ stomachs with food items) from individuals collected on highways in southern Brazil. %FO – frequency of occurrence, %N – contribution by number, %PN – prey-specific contribution by number, %M – contribution by mass, %PM – prey-specific contribution by mass, PSIRI% – prey-specific index of relative importance. %FO, %N, and %M were calculated considering all stomachs containing food items ($n = 17$), whereas %PN and %PM were calculated only from stomachs containing the respective prey item, as these measures represent its prey-specific contribution, as in Brown et al. (2012). Higher categories are marked in bold.

Food item	%FO	%N (%PN)	%M (%PM)	PSIRI%
Invertebrates				
Chelicerates	11.7	4.5	<0.1	6.3
Araneae	11.7	4.5 (57.1)	<0.1 (50.0)	6.3
Crustaceans	5.8	2.3	1.3	4.3
Brachyura	5.8	2.3 (50.0)	1.3 (98.1)	4.3
Insects	76.4	47.9	0.6	20.8
Gryllotalpidae	5.8	4.5 (16.6)	<0.1 (<0.1)	0.5
Tettigoniidae	5.8	2.3 (8.3)	<0.1 (<0.1)	0.3
Gryllidae	5.9	2.3 (100)	<0.1 (100)	5.8
Belostomatidae	5.8	2.3 (100)	0.1 (100)	5.8
Formicidae	5.8	13.6 (50.0)	<0.1 (0.1)	1.5
Apidae	5.8	2.3 (20.0)	<0.1 (<0.1)	0.6
Curculionidae	5.8	2.3 (20.0)	<0.1 (<0.1)	0.6
Elateridae	5.8	2.3 (14.2)	<0.1 (1.7)	0.5
Coleoptera 1	5.8	2.3 (14.2)	<0.1 (11.4)	0.7
Coleoptera 2	17.6	11.4 (37.6)	0.1 (12.1)	3.3
Lepidoptera	5.8	2.3 (33.3)	0.2 (6.8)	1.2
Vertebrates				
Fish	5.8	2.3	1.1	1.9
<i>Synbranchus marmoratus</i>	5.8	2.3 (50.0)	1.1 (15.9)	1.9
Amphibians	35.2	16.0	16.3	19.0
<i>Leptodactylus latrans</i>	11.8	6.8 (24.1)	12.0 (62.0)	5.1
<i>Leptodactylus</i> sp.	5.9	2.3 (100)	4.0 (100)	5.8
<i>Physalaemus</i> sp.	5.9	2.3 (100)	<0.1 (100)	5.8
<i>Boana pulchella</i>	5.8	2.3 (8.3)	0.1 (0.7)	0.4
<i>Boana</i> sp.	5.8	2.3 (14.2)	0.1 (52.3)	1.9
Reptiles	5.8	2.3	0.4	1.3
<i>Phalotris lemniscatus</i>	5.8	2.3 (33.3)	0.4 (12.6)	1.3
Birds	11.7	4.6	9.1	9.1
<i>Myiopsitta monachus</i>	5.8	2.3 (100)	6.5 (100)	5.8
<i>Molothrus bonariensis</i>	5.8	2.3 (33.3)	2.6 (80.5)	3.3
Mammals	52.9	20.6	70.5	35.7
Unidentified rodent	5.8	2.3 (50.0)	12.2 (84.0)	3.9
<i>Ctenomys torquatus</i>	5.8	2.3 (8.3)	6.6 (74.6)	2.5
<i>Scapteromys tumidus</i>	5.8	2.3 (100)	0.9 (100)	5.8
<i>Deltamys kempi</i>	5.8	2.3 (100)	43.6 (100)	5.8
<i>Holochilus vulpinus</i>	17.6	6.8 (66.6)	0.5 (97.0)	14.4
<i>Calomys laucha</i>	5.8	2.3 (50.0)	5.9 (3.3)	1.6
<i>Oligoryzomys</i> sp.	5.8	2.3 (50.0)	0.8 (5.4)	1.7

Rice grains were found in one specimen, not included in the list of food items due to probable secondary consumption.

specialization revealed differences in the degree of specialization between isotopes. Nitrogen showed an intermediate (0.4) and higher (0.7) WIC/TNW ratio, with TDF-corrected and uncorrected $\delta^{15}\text{N}$ values, respectively, indicating moderate individual specialization in trophic level. For $\delta^{13}\text{C}$ values, a much lower ratio (0.02 and 0.03, respectively) was found, suggesting consistent consumption of particular prey groups or prey mixtures among individuals (Table 3).

4. Discussion

The Great Horned Owl exhibited a generalist feeding habit in southern Brazil, preying upon a broad range of taxonomic groups, from invertebrates to vertebrates, consistent with previous reports for the species (Tomazzoni et al., 2004; van Damme, 2005; Dias and Kasper, 2023; Cisneros-Heredia et al., 2026). The presence of prey with low occurrence in stomachs analyzed reinforces its opportunistic foraging behavior, as already described for this owl (e.g., Cisneros-Heredia et al.,

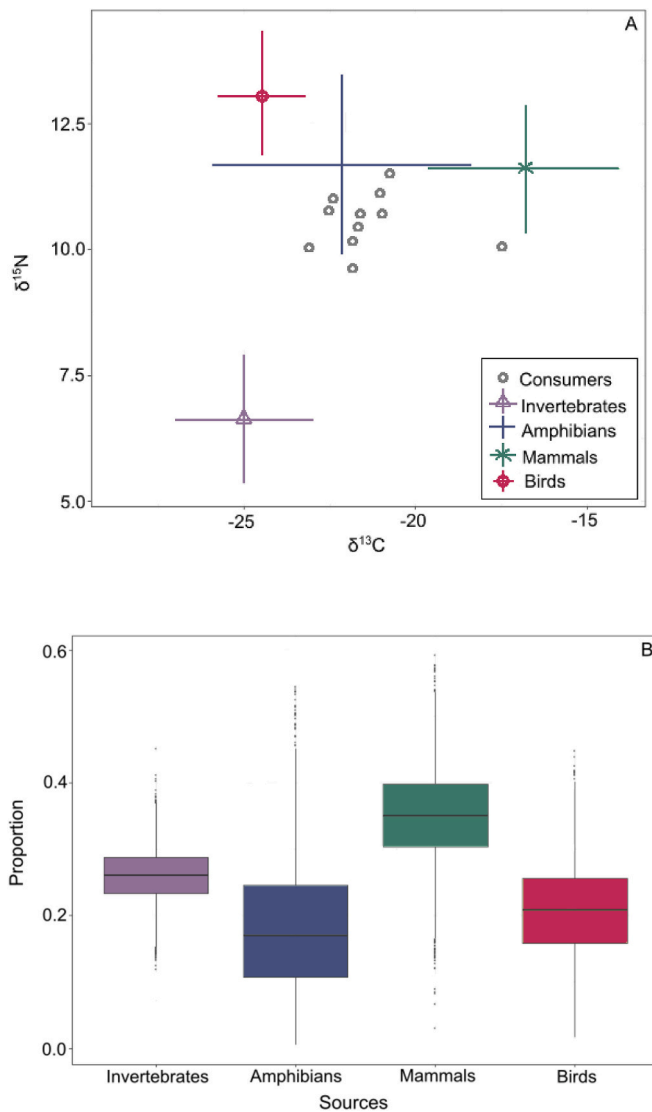


Fig. 2. (A) Biplot of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotope values (in ‰) of potential prey (insects, amphibians, mammals, and birds) and of Great Horned Owl (*Bubo virginianus*, $n = 12$) muscle tissue (Consumers). (B) Estimated proportions of potential prey contributing to muscle tissue synthesis of Great Horned Owl, based on Bayesian stable isotope mixing models. Trophic Discrimination Factors (TDFs) were applied to adjust prey isotope values prior to the mixing model analysis.

2026). In addition, stable isotope results indicated possible dietary individual specialization of the species. These findings highlight the remarkable ecological plasticity of the Great Horned Owl, which enables it to exploit a wide range of resources in human-modified landscapes.

Rodents were the most important prey group (PSIRI% = 35.7), corroborating previous studies (Bogiatto et al., 2003; Kopij, 2013; Dias and Kasper, 2023). The shared nocturnal activity pattern between owls and many rodent species likely enhances encounter rates (Teta et al., 2006), while the predominance of small rodents suggests an optimal balance between energetic reward and handling effort (Taylor, 2009). Invertebrates, although contributing less to biomass, represented the second most frequent prey group (PSIRI% = 20.8). Their abundance may result from ease of capture, short handling time, and favorable energetic return (Kremer and Belk, 2003), as already observed for the species (e.g., Šálek et al., 2010; Udrizar-Sauthier et al., 2017). Amphibians were another important prey group (PSIRI% = 19.0), mainly species of *Leptodactylus*, whose nocturnal activity and proximity to

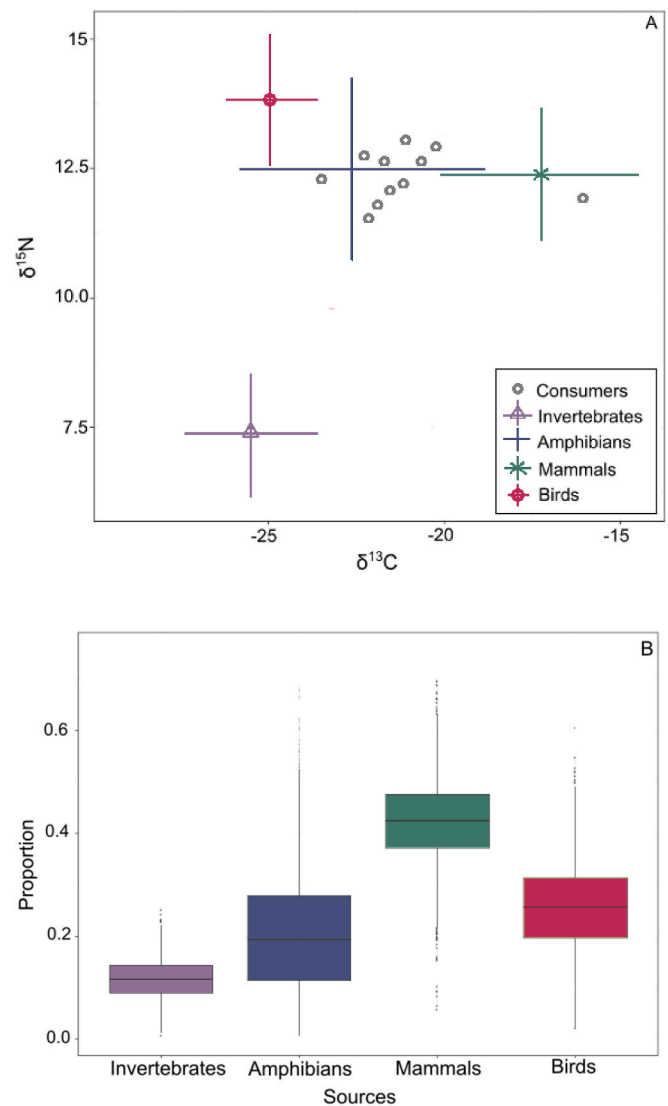


Fig. 3. (A) Biplot of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotope values (in ‰) of potential prey (insects, amphibians, mammals, and birds) and of Great Horned Owl (*Bubo virginianus*, $n = 12$) liver tissue (Consumers). (B) Estimated proportions of potential prey contributing to liver tissue synthesis of Great Horned Owl, based on Bayesian stable isotope mixing models. Trophic Discrimination Factors (TDFs) were applied to adjust prey isotope values prior to the mixing model analysis.

wetlands may explain their prevalence (França et al., 2004). The frequent occurrence of wetlands near roadkill sites, coupled with the high mortality of some amphibians on roads (Coelho et al., 2012), may also facilitate opportunistic predation or scavenging by owls. Other prey types, such as birds, reptiles, and fish, were less frequent, likely reflecting occasional or opportunistic consumption. The rice grains found in one individual's stomach probably represent secondary ingestion, possibly derived from a granivorous bird (*Myiopsitta monachus*) that may be consumed near highways used for rice transport, where grains are frequently spilled (Fernandez, 2016; South and Pruett-Jones, 2000).

Stable isotope analysis provided complementary insights into nutrient assimilation over recent temporal scales. Small mammals were the primary contributors to the synthesis of muscle, liver, and feather tissues, consistent with their predominance in the stomach content and other studies (Teta et al., 2006; Kopij, 2013; Cisneros-Heredia et al., 2026). Amphibians ranked second in importance, emphasizing the ecological relevance of wetland habitats for foraging. Birds also

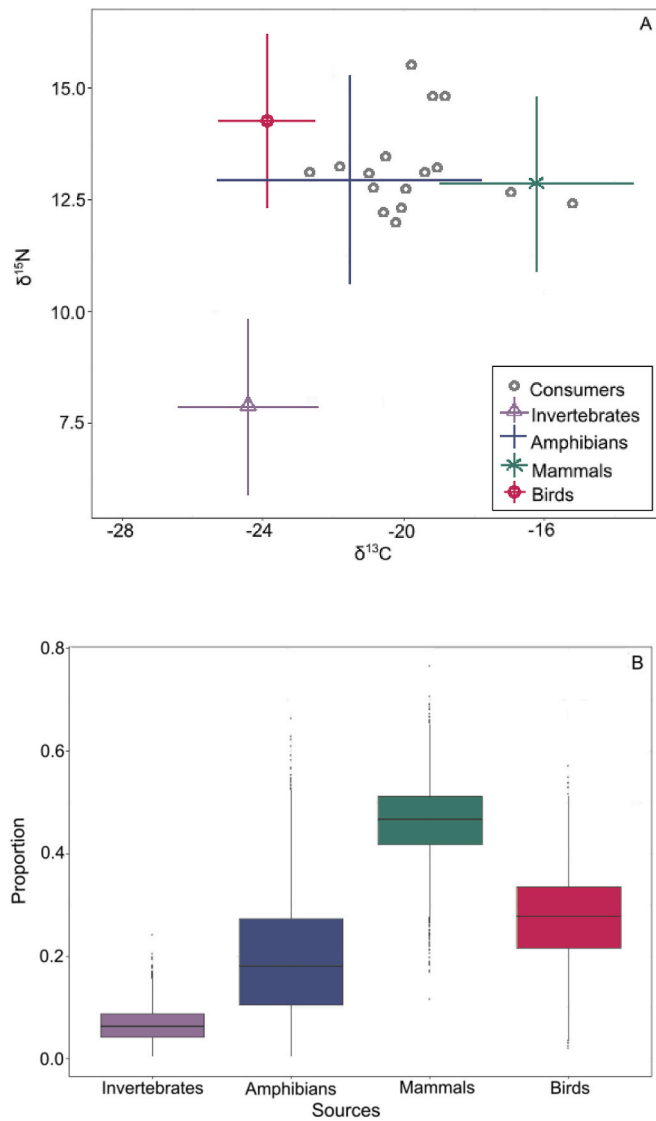


Fig. 4. (A) Biplot of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotope values (in ‰) of potential prey (insects, amphibians, mammals, and birds) and of Great Horned Owl (*Bubo virginianus*, $n = 16$) growing feathers (Consumers). (B) Estimated proportions of potential prey contributing to growing feathers synthesis of Great Horned Owl, based on Bayesian stable isotope mixing models. Trophic Discrimination Factors (TDFs) were applied to adjust prey isotope values prior to the mixing model analysis.

contributed notably to tissue synthesis, in agreement with previous dietary studies (Tomazzoni et al., 2004). Invertebrates showed a relatively lower overall contribution compared with other prey groups, but the mixing model estimated a higher proportional contribution of invertebrates to muscle tissue than to liver and feathers, indicating that they may still represent a relevant dietary component, particularly as a short-term energy source (Kremer and Belk, 2003).

Table 3

Values of the within-individual component (WIC), between-individual component (BIC), and total niche width (TNW) obtained through ANOVA of the Great Horned Owl (*Bubo virginianus*, $n = 7$) in southern Brazil. WIC/TNW values range from 0 to 1, with lower values indicating higher individual specialization. TDF – tissue specific trophic discrimination factors, used to correct isotopic values before calculations, as in Table S2.

	$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)			
	WIC	BIC	TNW	WIC/TNW	WIC	BIC	TNW	WIC/TNW
Non-corrected values	0.50	13.11	13.60	0.03	1.37	0.54	1.91	0.70
TDF-corrected values	0.37	13.14	13.51	0.02	0.35	0.54	0.89	0.40

Nitrogen isotope ratios reflected the owl's broad trophic niche, encompassing prey from multiple trophic levels, from low-trophic invertebrates to high-trophic vertebrates, corroborating the stomach content analysis. The WIC/TNW analysis based on uncorrected isotopic values suggested relatively low individual specialization (WIC/TNW = 0.70). However, after correcting isotopic values using tissue-specific trophic discrimination factors, the WIC/TNW ratio decreased to 0.40, indicating moderate individual specialization across trophic levels. Although spatial variation in baseline $\delta^{15}\text{N}$ values may also contribute to isotopic differences among individuals, the highly mobile foraging behavior of Great Horned Owls likely integrates prey from multiple habitats, reducing the influence of localized baseline variation. Carbon isotope ratios consistently indicated strong individual specialization regardless of TDF correction (WIC/TNW = 0.03 and 0.02 for uncorrected and corrected values, respectively), suggesting consistent consumption of different prey groups or prey mixtures among individuals. Spatial variation in baseline $\delta^{13}\text{C}$ values across the landscape may also contribute to this pattern and therefore cannot be excluded. Together, these isotopic patterns support the existence of individual dietary specialization in a generalist species, as also previously inferred for this owl (Duxbury and Holroyd, 1997), though prior studies did not assess carbon stable isotopes. Such specialization is challenging to detect in raptors (Nadjafzadeh et al., 2016) due to observational limitations (Whitfield et al., 2009). Nonetheless, it has been observed that the diet of Great Horned Owls that nest near colonies of Leach's Storm-Petrels (*Hydrobates leucorhous*) is mostly composed by these seabirds (Pollet and Shutler, 2019). However, this phenomenon can have ecological and conservation implications. In other birds, individual specialization has been linked to variation in reproductive success and body condition (Votier et al., 2010). Moreover, specialized individuals can be more vulnerable to environmental changes (Durell, 2000), as seen in Northern Gannets (*Morus bassanus*) that rely on fishery waste and are disproportionately affected by bycatch (Votier et al., 2010). For Great Horned Owls, individuals specializing in foraging near roads or on roadkilled food items may face elevated mortality risk due to vehicle collisions.

Owls are particularly susceptible to road mortality (Boves and Belthoff, 2012; Bishop and Brogan, 2013; Borda-de-Água et al., 2014), especially when moving between habitat fragments (König and Weick, 2008) or being attracted to roads by synanthropic prey or carrion (Anza and Zilio, 2015; Allen et al., 2019). The ability of Great Horned Owl to forage in open areas and consume synanthropic prey (e.g., rodents, birds) may increase its exposure to anthropogenic hazards. These findings reinforce the importance of evaluating individual-level ecological patterns when assessing the impacts of human-driven environmental changes on predator populations.

5. Conclusions

Our findings highlight the trophic plasticity of the Great Horned Owl in a human-modified landscape and reveal consistent individual-level specialization in prey use. Understanding such ecological variation is essential for developing effective conservation strategies, particularly in anthropogenic environments where generalist species may persist, yet specialized individuals remain vulnerable.

This study represents the first integrated assessment of the Great Horned Owl's diet combining stomach content and stable isotope

analyses, a methodological approach rarely applied to birds of prey due to the challenges of obtaining suitable samples through non-invasive methods or opportunistic sampling. The use of specimens and samples archived in museums, as used here, and the integration of these complementary techniques provided a more comprehensive understanding of the species' trophic ecology and resource use across a mosaic of natural and modified habitats. By comparing TDF-corrected and uncorrected stable isotopic values, we found similar results of WIC/TNW for carbon, but differences for the more variable nitrogen. Thus, we suggest the use of TDF-corrected values in studies of individual specialization. Findings also emphasize the importance of wetlands and road-influenced environments for owls in southern Brazil.

CRedit authorship contribution statement

Vitória Muraro: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Cynthia Negrine Fernandez:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Leandro Bugoni:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fooweb.2026.e00472>.

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