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PRIMARY RESEARCH PAPER

Diet and resource partitioning between egrets and herons in an estuarine colony in southern Brazil

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Abstract Herons are predators at high levels of the trophic webs in aquatic and adjacent terrestrial environments. They often breed sympatrically, forming colonies with multiple species that play key roles in the transport of nutrients and can serve as environmental sentinels. However, studies evaluating foraging habits, resource partitioning, and niche overlap are still scarce. We used complementary stable isotopes of carbon and nitrogen, and food remains analyses to investigate diet overlap among cattle egret (*Bubulcus ibis*), snowy egret (*Egretta thula*), and black-crowned night heron (*Nycticorax nycticorax*) at the Lagoa dos Patos estuary, southern Brazil. These species fed on vertebrates (mainly fish but also anurans and bird chicks) and arthropods (insects, arachnids, and crustaceans) in varying proportions. Similarly, stable isotopes demonstrated assimilated sources from estuarine, limnetic, and terrestrial areas, with food items differing in proportions. The diet of cattle egrets was composed mainly of terrestrial prey, while snowy egrets fed mainly on aquatic prey. Black-crowned night herons had a generalist diet and the highest isotopic niche breadth, which overlapped with other species. Our study demonstrated that small-to-medium-sized herons have trophic plasticity and despite sharing food items in different proportions, they show a distinction in at least one of the niche dimensions (temporal, spatial, or trophic), which allows for the coexistence of sympatric species in multispecies colonies.

Keywords *Bubulcus ibis* · *Egretta thula* · Feeding · *Nycticorax nycticorax* · Regurgitates · Stable isotopes

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Introduction

The composition of ecological communities, defined by species diversity and arrangement, is strongly influenced by abiotic and biotic factors (Begon et al., 2007; Mittelbach & McGill, 2019). The pool of *n*-dimensional environmental resources and conditions required by a species to exist is regarded as its niche (Hutchinson, 1957). The niche of a species can overlap among and within the niches of other species in a community (Gause, 1937). However, multiple species can still coexist under specific conditions without competing, but this coexistence depends on resource availability and strategies of the consumers (Gause, 1937; Schoener, 1974; Bearhop et al., 2004; Begon et al., 2007). Thus, studies on resource partitioning are important to understand the mechanisms that influence community structure and niche overlap (e.g., Comte et al., 2016; Faria et al., 2018; Salas-López et al., 2022; Navarro et al., 2023). Environments such as estuaries are recognized for their nutrient abundance (Day-Jr. et al., 2013) and integrate resources from marine, terrestrial, and freshwater ecosystems, providing feeding, breeding, and roosting sites for numerous bird species, including herons and egrets (Weller, 1999; Kushlan & Hancock, 2005; Kennish, 2019).

Herons and egrets often breed in colonies with sympatric species (Kushlan & Hancock, 2005). They use environments where food resources are abundant, a strategy known as central place foraging (Bell, 1990). These birds use diverse foraging techniques related to their body and bill morphology, typically capturing their prey with their bills while wading in shallow waters (Kushlan & Hancock, 2005). Cattle egrets [*Bubulcus ibis* (Linnaeus, 1758)], snowy egrets [(*Egretta thula* (Molina, 1782)], and black-crowned night herons [(*Nycticorax nycticorax* (Linnaeus, 1758)] are sympatric, small-to-medium-sized, predatory waterbirds (Kushlan & Hancock, 2005; Hothem et al., 2020; Parsons & Master, 2020; Telfair-II, 2023) and, therefore, with potential niche overlap and/or niche segregation.

The cattle egret is originally from Africa (Ducommun et al., 2008; Moralez-Silva & Del Lama, 2014) but now has colonized the New World due to its great capacity to invade and occupy new areas (Kushlan & Hancock, 2005; Nunes et al., 2010; Abdullahm et al., 2017). The species inhabits grasslands and benefits from insects that emerge from the soil with cattle movement (Bó & Darrieu, 1993; Kaufman, 1996; Kushlan & Hancock, 2005). Its variable diet includes insects, arachnids, and amphibians (Sánchez-García, 2012; Vega-Sánchez et al., 2022). The snowy egret has a wide distribution, occurring in aquatic environments throughout the Americas (Martínez-Vilalta & Motis, 1992; Brzorad & Maccarone, 2013). The species feeds mainly on fish, but crustaceans, amphibians, reptiles, and insects are also among their prey (Smith, 1997; Antón-Tello et al., 2021). The black-crowned night heron occurs in the Americas, Europe, Africa, and Asia (Hancock & Kushlan, 2010). It is considered an opportunistic species, foraging solitarily during the night or twilight (Kushlan & Hancock, 2005; Maccarone et al., 2015). As observed for cattle and snowy egrets, black-crowned night herons also have a varied diet, consuming items such as fish, amphibians, reptiles, small rodents, bats, insects, spiders, crustaceans, mollusks, birds (including cannibalism), and eggs of many other species (Kazantzidis & Goutner, 2005; Kushlan & Hancock, 2005; Riehl, 2006; Régale et al., 2014). These three species are often seen using habitats modified by humans such as artificially created vegetated banks, shallow freshwater environments used for irrigation of crops, saltwater rivers, man-made streams, lakes, and lagoons, and anthropically modified swamps and mangroves (Kushlan & Hancock, 2005).

Despite their substantial ecological influence in estuaries, where they facilitate nutrient transfer from aquatic to terrestrial ecosystems, subsidizing trophic interactions (Caseiro-Silva et al., 2023), detailed information on the diet and ecological roles of herons and egrets in these environments remains scarce. To understand the role of cattle egrets, snowy egrets, and black-crowned night herons in estuaries, their interspecific interactions and resource partitioning, food preferences, and energy and nutrient flow should be elucidated (Steinmetz et al., 2003; Green & Elmberg, 2014). These can be assessed through diet and isotopic niche studies.

Conventional diet studies can be applied and allow us to determine and quantify the prey consumed through the fragments found in regurgitates and pellets. Regurgitates represent partially

digested prey, while pellets are composed of hard remnants of undigested food items covered by mucus. Both regurgitates and pellets allow for estimates of the contribution of different food items in a consumer's diet, associated with niche metrics. These analyses provide essential background information for more advanced research techniques, such as stable isotopic analyses, enhancing the accuracy of isotopic mixture models (Layman et al., 2012; Parnell et al., 2013; Britto & Bugoni, 2015).

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes are commonly used to identify food resources assimilated in consumer tissues. This technique provides valuable insights into the prey species consumed, isotopic niche overlap, and isotopic niche breadth, allowing for a comparison across various trophic niche dimensions (Newsome et al., 2007; Layman et al., 2012; Hette-Tronquart, 2019). While $\delta^{13}C$ is particularly useful in identifying environmental sources of food, as it considers the photosynthetic cycle of primary C3 vs C4 producers, leading to a slight variation in consumer-tissue discrimination, $\delta^{15}N$ is more suitable for identifying trophic relationships, as it increases at each trophic level (Post, 2002; Staddon, 2004; Fry, 2006; Castro et al., 2016).

In this study, we examined trophic niche partitioning among three small-to-medium-sized estuarine herons and egrets that breed sympatrically, through complementary techniques, i.e., analyses of regurgitates, pellets, and stable isotopes. We hypothesized that cattle egrets would have a distinct niche as they forage mainly in terrestrial environments, compared to the other two species that feed mainly in aquatic environments. We further hypothesized that snowy egrets would have a restricted niche as they forage preferentially in coastal, estuarine, and limnetic environments. Finally, we hypothesized that black-crowned night herons would have the most diverse diet and high trophic and isotopic niche overlap. As cattle egrets have a predominantly terrestrial feeding habit, foraging primarily on insects available nearby nests, we expect that cattle egrets will occupy a lower trophic level in comparison to snowy egrets and black-crowned night herons, which are species that feed predominantly on carnivorous fish and crustaceans available in the aquatic environments. Conversely, we expect to find a higher trophic level and wider isotopic niche for black-crowned night herons compared to the egrets, reflecting their opportunistic feeding habits, which include animals of high trophic levels, such as predatory fish, birds, amphibians, and mammals.

Methods

Study area and field sampling

Bird sampling took place on Marinheiros Island (32°00′ S, 52°09′ W; Fig. 1), with 40 km^2, in the Lagoa dos Patos Estuary, Rio Grande city, Rio Grande do Sul, Brazil. The island is surrounded by a belt of wetland environments and composed of horticultural areas, swamp ('restinga') forests in the peripheral zone, dunes, and a lagoon in the center of the island (Gianuca et al., 2010). The climate in the region is temperate (Klein, 1997), with a variation of ambient temperatures from 5.9 to 35 °C during the spring of 2019 and from 12.8 to 35.9 °C in the summer of 2020 (INMET, 2023). The salinity and water level are influenced by climate and rainfall, with the highest salinity consistently occurring in summer (Garcia et al., 2001). The island is situated in an important region for the conservation of waterbirds (Williamson et al., 2013), and a colony of Pelecaniformes is established yearly in the restinga forest, a few hundred meters from the shore of Lagoa dos Patos (Gianuca et al., 2010; Britto & Bugoni, 2015; Barreto et al., 2025). This colony is the breeding site of two species of Threskiornithidae, the roseate spoonbill [*Platalea ajaja* Linnaeus, 1758 and the bare-faced ibis, *Phimosus infuscatus* (Lichtenstein, 1823)], and seven species of Ardeidae, the great egret (*Ardea alba* (Linnaeus, 1758)], the cocoi heron (*Ardea cocoi* (Linnaeus, 1766)], the cattle egret, the little blue egret [(*Egretta caerulea* (Linnaeus, 1758)], the snowy egret, the yellow-crowned night heron [(*Nyctanassa violacea* (Linnaeus, 1758)], and the black-crowned night heron (Gianuca et al., 2010; Barreto et al., 2025). The trees in which each species will nest in a particular year, as well as the nest height, seems to be related to arrival of breeding pairs, but does not have a particular species-specific pattern in multispecies colonies, although there is a tendency of bigger species (i.e., spoonbills, cocoi herons, and great egrets) arriving earlier and, therefore, nesting in

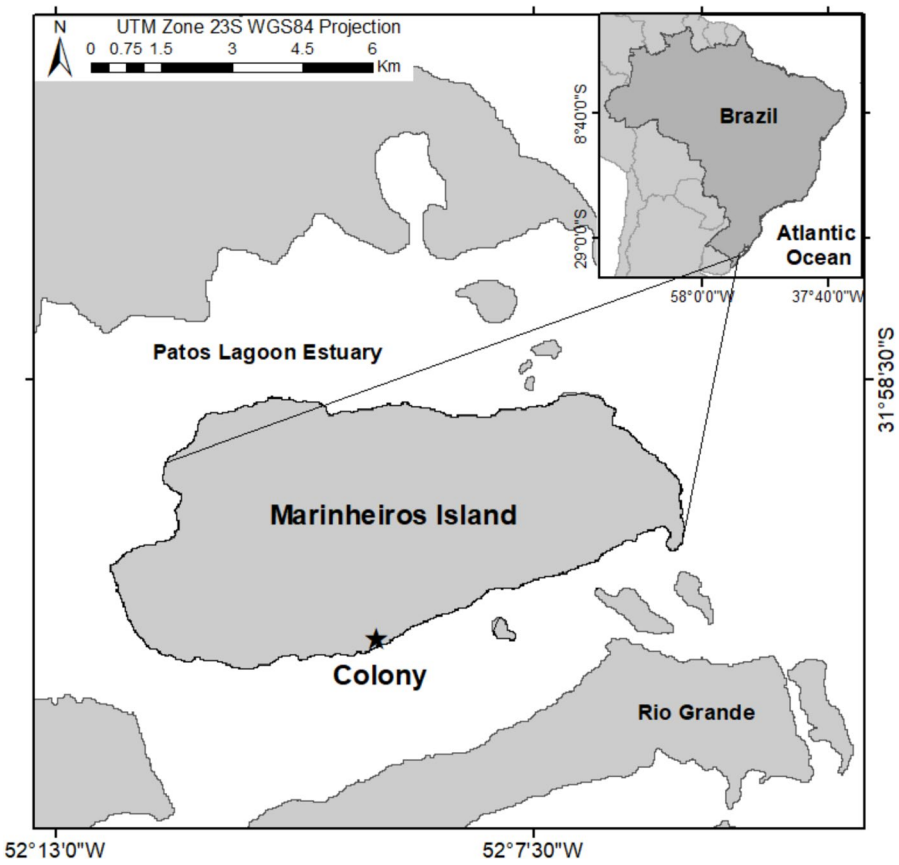

Fig. 1 Marinheiros Island, Lagoa dos Patos Estuary, southern Brazil. The star indicates the colony location where cattle egret (*Bubulcus ibis*), black-crowned night heron (*Nycticorax nycticorax*), and snowy egret (*Egretta thula*) breed annually. (Map courtesy of A.B. da Silva)

taller trees (Bachir et al., 2008, Gianuca et al., 2010; Park et al., 2011).

Spontaneous regurgitates and pellets were sampled from chicks of three ardeids (23 black-crowned night herons, six cattle egrets, and three snowy egrets) inside the nests or their surroundings, during the breeding season, between September 2019 and January 2020, for conventional analysis of the diet. Dietary samples were stored in plastic bags and frozen until analysis. For stable isotope analysis sampling, chicks were manually captured, morphometric measurements were taken to infer age, and approximately 0.1 mL of blood was drawn from their tarsal vein by using a syringe and needle. To avoid resampling, birds were banded with uniquely numbered metal bands provided by the Centro Nacional de Pesquisa e Conservação de Aves Silvestres (CEMAVE) of the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). Blood samples were preserved in 1.5 mL vials in the field, taken to the Waterbirds and Sea Turtles Laboratory (LAATM) of the Universidade Federal do Rio Grande (FURG), and frozen until analysis. Only chicks at least 3 weeks old were sampled, as it is expected that due to the turnover time range of 7–20 days (Boecklen et al., 2011), the isotopic composition of the blood will represent values of the food delivered by parents rather than egg nutrients. A total of 43 samples from different individuals were collected for stable isotope analysis (15 cattle egrets, 20 black-crowned night herons, and eight snowy egrets). Additionally, insects of the orders Orthoptera, Odonata, and Coleoptera and spiders, to represent the isotopic values of consumed invertebrates, were collected manually. Finally, whole or minimally digested fish present in the regurgitates had tissues sampled to represent the isotopic values of limnetic and estuarine fish consumed.

Conventional diet data analysis

To identify the consumed prey, items found in the samples were separated by washing the regurgitates

and pellets under running water in a 0.75 mm mesh metal sieve. Intact prey items were separated from other food items (parts of prey items). All consumed food items were quantified (i.e., counted), measured in millimeters with a caliper, and weighed in grams on a laboratory scale. For identification, items were examined under a stereomicroscope, and prey items were compared with reference collections and identification guides (Fisher et al., 2004; Malabarba et al., 2013; Conversani et al., 2017; Hamada et al., 2018).

For each prey species, the relative frequency of occurrence (FO%), which is the presence of the taxon related to the total number of samples, the mean percentage contribution of each food item (PN%), and the percentage contribution of the reconstituted mass of each food item (PM%) were calculated. Prey mass was reconstructed using allometric equations based on measurements of fish otoliths or from mean values of similar-sized prey (Bugoni & Vooren, 2004). Due to the low sample size of snowy egrets, dietary parameters were calculated only for cattle egrets and black-crowned night herons. After obtaining FO%, PN%, and PM%, we calculated the prey-specific relative importance index (PSIRI%) according to Brown et al. (2012):

$$\mathrm{PSIRI\%} = \left[\mathrm{FO\%} \times \left(\mathrm{PN_i\%} + \mathrm{PM_i\%}\right)\right]/2 \quad (1)$$

where FO% is the frequency of occurrence of each taxon; PNi% is the contribution in number of each taxon; and PMi% is the mass contribution of each taxon.

To calculate the trophic niche overlap among species, based on the contribution in numbers of each taxon (N%), we used the Morisita-Horn similarity index (Horn, 1966), following the equation:

$$\mathrm{CH} = \left[2\left(\Sigma ni \times p_{ij} \times p_{ik}\right)\right]/(\Sigma ni \times p2ij + \Sigma ni \times p2ik) \quad (2)$$

where CH is the Morisita-Horn similarity index; n is the total number of resources used; p_{ij} is the proportion of resources i to the total resources used by species j and p_{ik} is the proportion of resource i on the total resources used by species k.

For the trophic niche breadth, which is based on the contribution in number of each taxon, we used the Levin's standardized index (Magurran, 2019), following the equation of Hurlbert (1978):

$$\mathrm{Bs} = [(\Sigma pi^2) - 1]/(n-1) \quad (3)$$

where Bs is Levin's standardized index; p_i^2 is the proportion of the resource belonging to resource category i; and n is the total number of food items consumed.

Stable isotope analysis (SIA)

In the laboratory, whole blood samples were freeze-dried, homogenized, and weighed in tin capsules. Insects, spiders, crabs, anurans, and fish samples from the regurgitates were placed in a Soxhlet extractor with petroleum ether for 6 h for lipid removal (Post et al., 2007; Elliott et al., 2017; Cloyed et al., 2020). Subsequently, the prey samples were freeze-dried, homogenized, and weighed in tin capsules. Blood and prey samples were then analyzed with an isotope ratio mass spectrometer (IRMS) coupled to an elemental mass analyzer at the Integrated Analysis Center at FURG (CIA-FURG, Brazil). The isotopic signature values are expressed by the delta notation (δ), in parts per thousand (‰), and differences between the stable isotope values of the sample compared to standards are given by Eq. 4, from Bond & Hobson (2012):

$$\delta^{13}\mathrm{C\,or}\,\delta^{15}\mathrm{N}\,(‰) = \left(R_{\mathrm{sample}}/R_{\mathrm{standard}}\right) - 1 \quad (4)$$

where δ^{13}C is the carbon stable isotope; δ^{15}N is the nitrogen stable isotope; R_{sample} is the ratio between the heavy and light isotopes of the sample; and R_{standard} is the ratio between the heavy and light isotopes of the standard. Glutamic acid, caffeine, and acetazolamide were the internal standards at CIA, and Vienna Pee Dee Belemnite limestone and air were carbon and nitrogen, respectively, as calibration standards. The internal standards had a deviation of 0.1‰ for δ^{13}C and 0.4‰ for δ^{15}N. For prey taxonomic groups not found in regurgitated samples nor sampled at the colony, isotopic data from the LAATM-FURG isotopic database were used.

Bayesian isotopic mixing models were generated on 'simmr' R package (Parnell et al., 2013) in R software version 4.0.1 (R Core Team, 2020) to estimate the contribution of food items in the whole blood of chicks. For the models, the most common prey found in regurgitates and pellets were used. The trophic discrimination factors (TDF) of the consumers in the models were -0.3 ± 0.5‰ and 2.61 ± 0.5‰

for $\delta^{13}C$ and $\delta^{15}N$, respectively, as they were used in previous studies with isotopic modeling at the same or closely related waterbirds (Silva-Costa & Bugoni, 2013; Britto & Bugoni, 2015; Faria et al., 2016). These TDFs were obtained from experimental studies with penguins, which are predominantly piscivorous birds that feed on whole fish [king penguin *Aptenodytes patagonicus* J.F. Miller, 1778: $\delta^{13}C = -0.81‰$ and $\delta^{15}N = 2.07‰$; southern rockhopper penguin *Eudyptes chrysocome* (J.R. Forster, 1781): $\delta^{13}C = 0.20‰$ and $\delta^{15}N = 2.72‰$; Cherel et al., (2005)], and from experiments with tufted puffins [*Fratercula cirrhata* (Pallas, 1769): $\delta^{13}C = -0.30$ and $\delta^{15}N = 3.05‰$; Williams et al., (2007)]. Finally, standard ellipse areas adjusted for small sample sizes (SEAc) were used to determine the isotopic niche breadth and overlap of isotopic niches of the three consumers using the stable isotope Bayesian ellipses in R (Jackson et al., 2011).

Results

Conventional diet analysis and trophic niche characterization

The analysis of regurgitates and pellets indicates a cattle egret diet composed mainly of insects, spiders, and anurans, but fish, crustaceans, and ticks (Table 1). The most frequent food items were insects (FO% = 100), which had an importance (PSIRI%) of 43.2, followed by anurans (FO% = 83.3%; PSIRI% = 26.6), and arachnids (FO% = 83.3%; PSIRI% = 13.0). Anurans and insects had the highest contribution, according to the percentage of their reconstituted mass (PM%), in the diet of cattle egrets (52.1% and 27.4%, respectively). The trophic niche breadth was Bs = 0.12.

The conventional analysis indicates a variety of items composing the diet of black-crowned night herons, which consists of insects, crustaceans, fish, spiders, tadpoles, and heron chicks, including cannibalism (Table 1). Insects (FO% = 78.2) and fish (FO% = 73.9) were the most frequently occurring prey. Notwithstanding, the highest contributions to reconstituted mass were bird chicks (PM% = 44.1), followed by fish (PM% = 29.1), while the most

Table 1 Mean values of $\delta^{13}C$ and $\delta^{15}N$ (‰ ± standard deviation) in the blood of chicks of the cattle egret (*Bubulcus ibis*), the black-crowned night heron (*Nycticorax nycticorax*), and the snowy egret (*Egretta thula*), and muscle/whole individual of potential prey from southern Brazil, used in the Bayesian mixing models. *n* = the number of samples analyzed

Birds and potential sources	Species/taxon	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	*n*	References
Chick blood	*Bubulcus ibis*	−22.47 ± 2.53	7.17 ± 0.78	15	This study
	Egretta thula	−23.77 ± 2.26	8.25 ± 0.35	8	This study
	Nycticorax nycticorax	−22.87 ± 2.64	9.91 ± 1.91	20	This study
Anurans		−23.31 ± 1.06	4.22 ± 0.82	5	This study
	Pseudis minuta	−24.77	5.18	1	This study
	Scinax squalirostris	−23.90	4.32	1	This study
	Physalaemus gracilis	−22.63 ± 0.71	3.87 ± 0.83	3	This study
Estuarine fishes	*Atherinella brasiliensis*	−14.61	12.29	2	Garcia et al. (2007)
Freshwater fishes	*Astyanax* sp.	−20.25 ± 1.9	11.82 ± 0.3	2	Garcia et al. (2007)
Crustaceans	*Callinectes* sp.	−18.68 ± 0.14	8.36 ± 1.63	2	This study
Aquatic insects	Belostomatidae	−28.3	5.7	1	Britto & Bugoni (2015)
Terrestrial insects		−25.67 ± 1.91	5.89 ± 1.96	6	
	Coleoptera	−25.65 ± 2.97	5.97 ± 2.20	3	This study
	Odonata	−25.34	5.09	1	LAATM database[a]
	Orthoptera	−25.88 ± 0.66	6.17 ± 2.96	2	This study and LAATM database

[a] Unpublished data

Table 2 Diet composition of chicks of the cattle egret (*Bubulcus ibis*) and the black-crowned night heron (*Nycticorax nycticorax*) at the colony of Marinheiros Island, Lagoa dos Patos Estuary, Brazil

Food items	Cattle egret ($n=6$)				Black-crowned night heron ($n=23$)			
	FO%	PN%	PM%	PSIRI%	FO%	PN%	PM%	PSIRI%
Anurans	**83.3**	**12.4**	**52.1**	**26.6**	**4.3**	**5.8**	**0.06**	**0.1**
Hylidae	66.6	9.7	41.7	17.0	–	–	–	–
Hypsiboas pulchellus	16.6	0.3	0.3	<0.1	–	–	–	–
Pseudis minuta	33.3	5.8	14.3	3.3	–	–	–	–
Scinax squalirostris	33.3	3.7	27.1	5.0	–	–	–	–
Leiuperidae	50.0	2.1	1.6	0.9	–	–	–	–
Physalaemus gracilis	33.3	1.8	1.4	0.5	–	–	–	–
Pseudopaludicola falcipes	16.6	0.3	0.2	<0.1	–	–	–	–
Leptodactylidae	33.3	0.5	8.8	1.5	–	–	–	–
Leptodactylus gracilis	16.6	0.3	0.7	<0.1	–	–	–	–
Leptodactylus latrans	16.6	0.3	8.0	0.7	–	–	–	–
Unidentified	–	–	–	–	4.3	5.8	0.06	0.1
Fishes	**16.6**	**5.3**	**4.8**	**0.8**	**73.9**	**12.1**	**29.1**	**15.2**
Atherinopsidae	–	–	–	–	30.4	3.9	23.1	4.1
Atherinella brasiliensis	–	–	–	–	30.4	3.9	23.1	4.1
Characidae	–	–	–	–	8.7	0.8	0.2	<0.1
Astyanax sp.	–	–	–	–	4.3	0.4	0.2	<0.1
Pseudocorynopoma doriae	–	–	–	–	4.3	0.4	0.04	<0.1
Poeciliidae	16.6	5.3	4.8	0.8	8.7	0.8	0.1	<0.1
Phalloceros caudimaculatus	16.6	5.3	4.8	0.8	8.7	0.8	0.1	<0.1
Cichlidae	–	–	–	–	4.3	0.4	0.09	<0.1
Sciaenidae	–	–	–	–	4.3	0.4	0.3	<0.1
Stellifer sp.	–	–	–	–	4.3	0.4	0.3	<0.1
Ariidae	–	–	–	–	4.3	0.8	0.8	<0.1
Genidens barbus	–	–	–	–	4.3	0.8	0.8	<0.1
Loricariidae	–	–	–	–	8.7	0.8	0.8	<0.1
Loricariichthys anus	–	–	–	–	8.7	0.8	0.8	<0.1
Synbranchidae	–	–	–	–	8.7	0.8	1.0	<0.1
Synbranchus marmoratus	–	–	–	–	8.7	0.8	1.0	<0.1
Unidentified	–	–	–	–	17.4	2.3	2.8	0.4
Birds	**–**	**–**	**–**	**–**	**8.7**	**0.8**	**44.1**	**1.9**
Ardeidae	–	–	–	–	8.7	0.8	44.1	1.9
Bubulcus ibis (chicks)	–	–	–	–	4.3	0.4	20.7	0.4
Nycticorax nycticorax (chicks)	–	–	–	–	4.3	0.4	23.4	0.5
Insects	**100.0**	**58.9**	**27.4**	**43.2**	**78.3**	**57.0**	**5.2**	**24.3**
Blattaria	50.0	2.9	1.4	2.6	4.3	0.4	0.04	<0.1
Blattidae	16.6	1.3	0.2	0.1	–	–	–	–
Coleoptera	66.6	13.9	2.1	5.3	56.5	41.0	3.8	12.6
Coccinellidae	16.6	0.3	0.2	<0.1	–	–	–	–
Eriopis connexa	16.6	0.3	0.2	<0.1	–	–	–	–
Hydrophilidae	–	–	–	–	4.3	0.4	0.04	<0.1
Scarabaeidae	–	–	–	–	4.3	0.4	0.04	<0.1
Diptera	66.6	15.3	9.3	8.1	–	–	–	–
Brachycera	66.6	7.9	5.1	4.3	–	–	–	–

Table 2 (continued)

Food items	Cattle egret ($n=6$)				Black-crowned night heron ($n=23$)			
	FO%	PN%	PM%	PSIRI%	FO%	PN%	PM%	PSIRI%
Dolichopodidae	16.6	0.5	0.3	<0.1	–	–	–	–
Muscidae	16.6	0.5	0.3	<0.1	–	–	–	–
Sarcophagidae	33.3	5.0	3.0	1.3	–	–	–	–
Tabanidae	16.6	0.8	0.5	0.1	–	–	–	–
Nematocera	16.6	0.5	0.3	<0.1	–	–	–	–
Tipulidae	16.6	0.5	0.3	<0.1	–	–	–	–
Hemiptera	50.0	2.6	1.4	1.0	39.1	6.2	0.6	2.6
Auchenorrhyncha	–	–	–	–	21.7	2.7	0.2	0.3
Cercopidae	–	–	–	–	8.7	1.6	0.1	<0.1
Heteroptera	33.3	1.0	0.6	0.3	17.3	1.9	0.2	0.18
Belostomatidae	33.3	0.5	0.3	0.1	13.0	1.6	0.1	0.1
Belostoma sp.	16.6	0.3	0.2	<0.1	4.3	0.8	0.07	<0.1
Pentatomidae	16.6	0.5	0.3	<0.1	–	–	–	–
Naucoridae	–	–	–	–	4.3	0.4	0.04	<0.1
Hymenoptera	50.0	1.0	0.8	0.5	30.4	7.0	0.6	1.1
Formicidae	16.6	0.3	0.2	<0.1	8.7	0.8	0.07	<0.1
Camponotus sp.	–	–	–	–	4.3	0.4	0.04	<0.1
Solenopsis invicta	16.6	0.3	0.3	<0.1	–	–	–	–
Neuroptera	33.3	0.8	0.6	0.2	–	–	–	–
Odonata	33.3	2.4	1.4	0.6	4.3	1.6	0.1	<0.1
Coenagrionidae	16.6	0.5	0.3	<0.1	–	–	–	–
Libellulidae	33.3	1.8	1.3	0.5	4.3	1.6	0.1	<0.1
Orthoptera	66.6	20.0	12.2	10.6	4.3	1.2	0.1	<0.1
Acrididae	50.0	3.9	2.4	1.6	–	–	–	–
Aleuas sp.	16.6	0.3	0.2	<0.1	–	–	–	–
Gryllidae	50.0	7.4	4.5	3.0	–	–	–	–
Tettigoniidae	33.3	5.3	1.6	1.1	–	–	–	–
Romaleidae	16.6	0.5	0.3	<0.1	4.3	1.2	0.1	<0.1
Alcamenes clarazianus	16.6	0.5	0.3	<0.1	4.3	1.2	0.1	<0.1
Arachnids	**83.3**	**16.6**	**14.7**	**13.0**	**17.3**	**6.6**	**0.9**	**0.6**
Araneae	83.3	15.5	14.3	12.4	17.3	6.6	0.9	0.6
Ixodidae	33.3	1.0	0.4	0.2	–	–	–	–
Rhipicephalus sanguineus	16.6	0.8	0.3	0.1	–	–	–	–
Crustaceans	**33.3**	**1.6**	**1.0**	**0.4**	**21.7**	**17.6**	**20.6**	**4.1**
Decapoda	–	–	–	–	13.0	4.3	18.1	1.4
Grapsidae	–	–	–	–	4.3	0.4	0.4	<0.1
Portunidae	–	–	–	–	8.7	1.6	17.8	0.8
Callinectes sp.	–	–	–	–	8.7	1.6	17.8	0.8
Isopoda	33.3	1.6	1.0	0.4	8.7	13.3	1.2	0.6
Ligiidae	33.3	1.6	1.0	0.4	8.7	13.3	1.2	0.6
Ligia exotica	33.3	1.6	1.0	0.4	8.7	13.3	1.2	0.6
		$n=380$			$n=256$			

FO% = frequency of occurrence; PN% = contribution in prey-specific numbers; PM% = contribution in prey-specific reconstituted mass; PSIRI% = prey-specific relative importance index. n = the number of samples analyzed

important prey were insects (PSIRI% = 24.3) and fish (PSIRI% = 15.2). The trophic niche breadth was Bs = 0.63. The niche overlap between black-crowned night herons and cattle egrets was high (CH = 0.67; Table 2), demonstrating an elevated overlap.

Snowy egret ($n = 3$) regurgitates indicated a diet composed of two killifish (i.e., small freshwater annual fish) species [*Phalloceros caudimaculatus* (Hensel, 1868) and *Cnesterodon decemmaculatus* (Jenyns, 1842)], three unidentified fish, and two insect groups (Belostomatidae and Odonata). Due to the low sample size, snowy egrets were not considered in the niche overlap analysis.

Prey assimilation and isotopic niche

Values for $\delta^{13}C$ and $\delta^{15}N$ in the blood of black-crowned night herons were more variable in comparison to the other two species, while values from snowy egret chicks were less variable (Table 1; Fig. 2). Mean $\delta^{13}C$ value in the blood of snowy egrets was −23.5‰, while the mean value for cattle egrets was −22.7‰ and for black-crowned night herons −22.9‰. The highest values of $\delta^{15}N$, on the other hand, were from the blood of black-crowned night heron chicks (9.9‰), followed by blood from snowy egrets (8.2‰), and cattle egrets (7.2‰).

As observed in the reconstituted mass analysis of cattle egrets ($n = 15$), stable isotopes mixing models indicated that anurans were their main food source (95% CI—credible interval = 10–90), followed by terrestrial insects (95% CI 0.8–21; Fig. 3a). For black-crowned night herons ($n = 20$), the stable isotopes mixing models indicated anurans (95% CI 4–57) and terrestrial insects (95% CI 2.4–55) as the resources most assimilated (Fig. 3b), contrasting the reconstituted mass results (from the conventional analysis of regurgitates) for the species. Finally, for snowy egrets ($n = 8$), anurans (95% CI 11–73) and aquatic insects (95% CI 2.8–60) were the most assimilated prey sources (Fig. 3c).

Regarding the isotopic niche (Table 2; Fig. 4), black-crowned night herons had the largest niche breadth (SEAc = 93.4), followed by cattle egrets (SEAc = 29.6), and snowy egrets with the lowest niche breadth (SEAc = 7.8). The isotopic niche of cattle egrets overlapped substantially (73.8%) with black-crowned night herons, but only 17% with snowy egrets. The niche of snowy egrets, on the other hand, overlapped only 8.3% with black-crowned night herons. The most surprising result was for the niche area of black-crowned night herons, which overlapped 100% with the niche area of snowy egrets and 73.8% with cattle egrets.

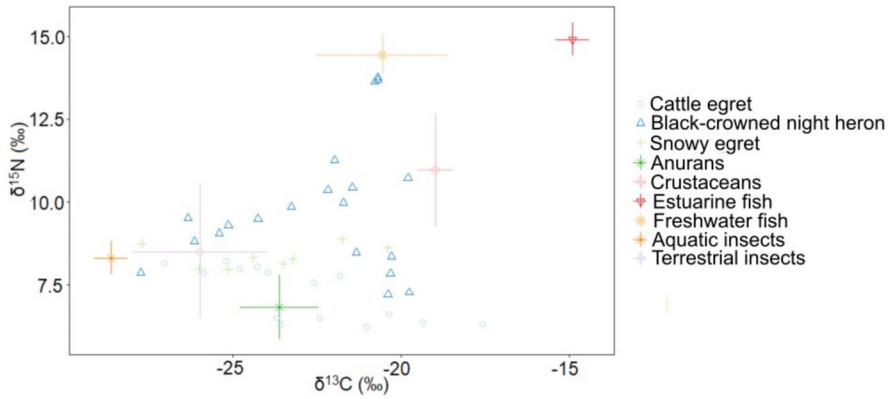

Fig. 2 Individual values of $\delta^{13}C$ and $\delta^{15}N$ (‰) in chick blood of cattle egret (*Bubulcus ibis*), black-crowned night heron (*Nycticorax nycticorax*), and snowy egret (*Egretta thula*). The means ± SD of isotopic values in their prey are from the estuarine environment, represented by estuarine fish (i.e., the Brazilian silverside *Atherinella brasiliensis*) and crustaceans (*Callinectes* sp.). Prey from the limnetic environment are represented by freshwater fishes (*Astyanax* sp.) and aquatic insects (Belostomatidae). Terrestrial prey are represented by anurans (i.e., *Pseudis minuta*, *Physalaemus gracilis*, and *Scinax squalirostris*) and terrestrial insects (Coleoptera, Odonata, and Orthoptera)

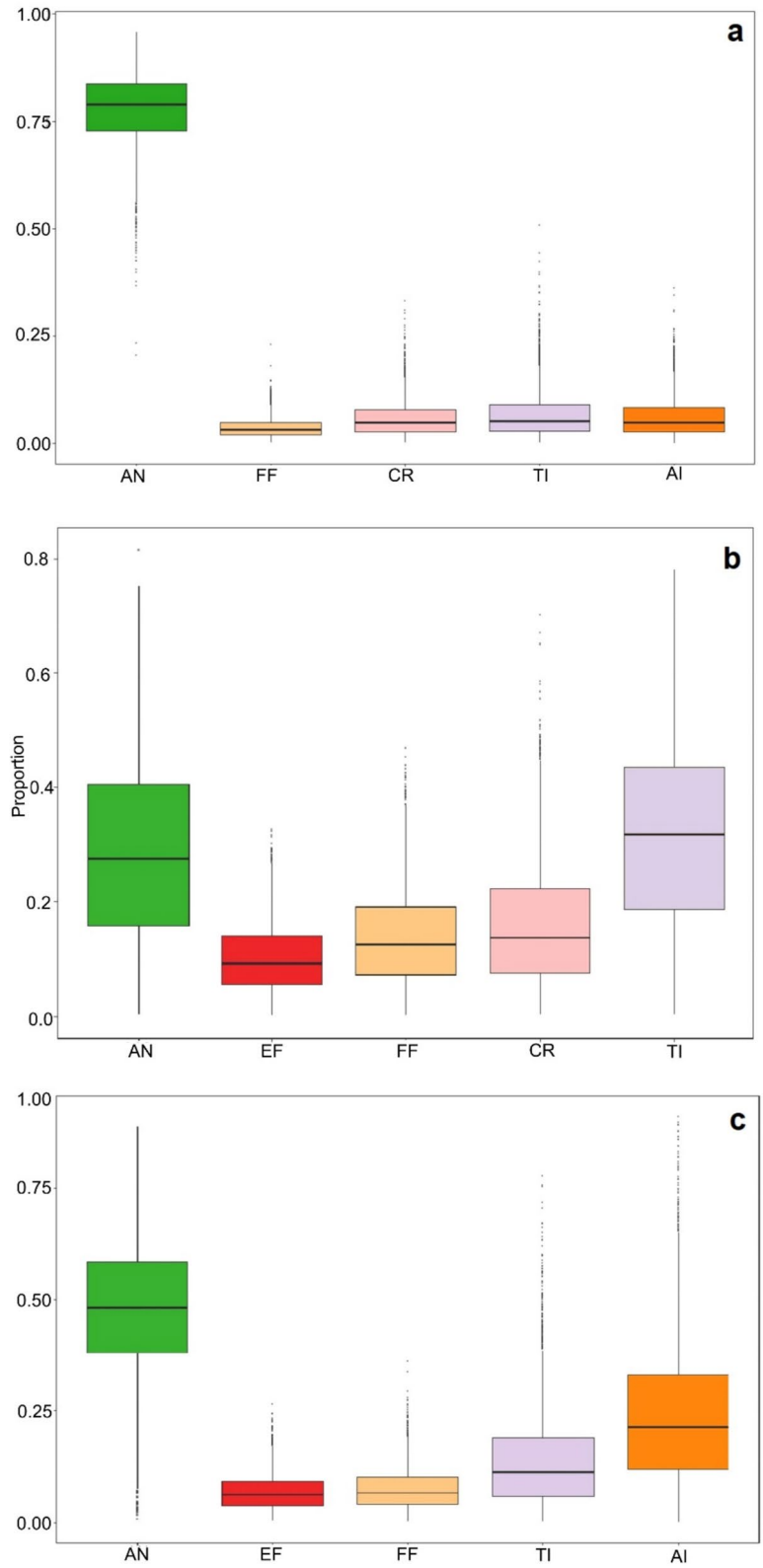

Fig. 3 Contribution of potential prey sources (AN = anurans, EF = estuarine fishes, FF = freshwater fishes, AI = aquatic insects, TI = terrestrial insects, and CR = crustaceans) as evidenced in the chick blood of (**a**) cattle egret (*Bubulcus ibis*), (**b**) black-crowned night heron (*Nycticorax nycticorax*), and (**c**) snowy egrets (*Egretta thula*) in an estuarine colony of Pelecaniformes on Marinheiros Island, Lagoa dos Patos Estuary, southern Brazil. The horizontal line in the center of the rectangle represents the mean, and the rectangle indicates the standard deviation. The vertical lines outside the rectangle indicate the minimum and maximum contribution values

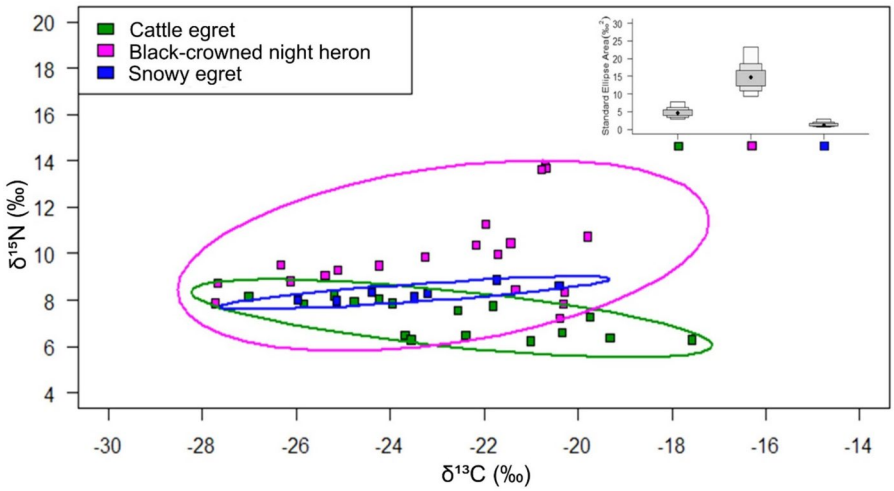

Fig. 4 Isotopic niche of cattle egret (*Bubulcus ibis*), black-crowned night heron (*Nycticorax nycticorax*) and snowy egret (*Egretta thula*) in delta space (δ) on Marinheiros Island, Lagoa dos Patos Estuary, southern Brazil, obtained through corrected standard ellipse areas (SEAc). The inset shows SEAc at $‰^2$ based on isotopic values in whole blood

Discussion

The three ardeids studied in southern Brazil had substantial overlap in their diet and trophic niches. Anurans were the most assimilated sources for all three species according to SIA, while insects were the most important food items in the diet of cattle egrets and black-crowned night herons according to pellet and regurgitation analysis. As demonstrated by δ^{15}N values, cattle egrets were at the lowest trophic level, followed by snowy egrets, and black-crowned night herons, matching our predictions. The diet of cattle egrets was mainly composed by terrestrial insects, matching our hypothesis of a terrestrial niche for the species. Snowy egrets had a more aquatic diet, composed mainly of fish and aquatic insects, which matches our hypothesis of a more restricted aquatic niche for the species. Black-crowned night herons had the most generalist feeding habit and most diverse diet, as well as the largest overlap of trophic niche with cattle egrets and isotopic niche with cattle and snowy egrets, marching our hypothesis of high trophic level and extensive niche overlap.

The Lagoa dos Patos Estuary is a relevant area for the conservation of Pelecaniformes in South America (Kushlan & Hancock, 2005; Dias et al., 2017) and has a high abundance of species that serve as food resources for birds (Pereira & D'Incao, 2012; Haimovici & Cardoso, 2016; Teixeira-Amaral et al., 2017; Lemos et al., 2022). The conventional diet analysis provided detailed information about the prey consumed by small herons and egrets from Marinheiros Island, similar to findings of other Pelecaniformes species in the same colony (Britto & Bugoni, 2015). Pellets and regurgitates, therefore, proved to be a reliable technique to determine the differences in food resources used by sympatric waterbird species breeding in heterogeneous environments.

The mainly terrestrial diet of cattle egrets diet corroborates with other studies (Ashoori et al., 2017a, b; Antón-Tello et al., 2021), predominantly insects, but also with varied taxa (Diptera, Orthoptera, and Hemiptera), in addition to small anurans and spiders, indicating that terrestrial environments near the colony were the main foraging areas for cattle egrets. Aquatic prey, including killifishes, and semiaquatic prey, such as giant waterbugs, were also present in the cattle egret diet, although consumed less frequently. Our results point to an opportunistic feeding habit, demonstrating that cattle egrets can be highly adaptive and explore both aquatic and terrestrial environments, similarly to the opportunistic feeding habits previously found (Kioko et al., 2016). Regarding the assimilation of consumed food items, isotopic results differed from a study in Spain (Antón-Tello et al., 2021), which showed insects as the main assimilated prey items for cattle egrets, followed by anurans. At Lagoa dos Patos, cattle egrets had anurans as the predominant assimilated food source, followed by terrestrial insects. Our models also indicated that cattle egrets have narrow trophic and isotopic niches due to the exploitation of predominantly terrestrial prey. This supports our hypothesis that the species has a

distinct niche because it forages primarily in terrestrial environments associated with cattle.

Black-crowned night herons also have a generalist feeding habit, matching our hypothesis of foraging in terrestrial, limnetic, and estuarine environments, with insects (Coleoptera, Hemiptera, and Hymenoptera) and fish of different sizes, such as the Brazilian silverside [*Atherinella brasiliensis* (Quoy & Gaimard, 1825)], as their main prey. Insects are among the most consumed prey items by black-crowned night herons elsewhere (e.g., Kazantzidis & Goutner, 2005), but fish are the most important prey in wetland areas (e.g., Ashoori et al., 2017a, b; Dias et al., 2025) as amphibians are in rice plantations (e.g., Cardarelli et al., 2017). Fish is an important prey for other Pelecaniformes breeding nearby the Lagoa dos Patos Estuary (Britto & Bugoni, 2015; Faria et al., 2016), and a variety of species of different sizes are present in both estuarine and limnetic areas in or near our study site (Quintela et al., 2018). Heron chicks, tadpoles, crustaceans, and spiders were also among the important food items consumed by black-crowned night herons in our study. Cannibalism by adults and juveniles feeding on chicks, which we detected in our samples, is reported in other studies (e.g., Riehl, 2006; Brussee et al., 2017; Sovrano et al., 2022), confirming the opportunistic behavior of the species (Davis-Jr., 1993). Regarding the taxa we found in the diet of black-crowned night herons, they were previously reported in South America in the Paraná River, Argentina (Quiroga et al., 2013). Our study found a more diverse diet of black-crowned night herons compared to other studies worldwide (review in Hothem et al., 2020), which can be explained by their opportunistic feeding behavior (Kazantzidis & Goutner, 2005) and foraging habits in varied environments (Dias et al., 2025). The SIA demonstrated that black-crowned night herons assimilated more sources from estuarine environments, such as fish and crustaceans, in addition to other sources from terrestrial and limnetic environments, distinct from the much narrower isotopic niche reported in a mixed colony at the New York/New Jersey Harbor Estuary (Craig et al., 2015). Results presented here confirmed our hypothesis that black-crowned night herons had the widest range of trophic and isotopic niches compared to egrets, as well as the greatest variety of taxa preyed upon.

For snowy egrets, two freshwater killifishes, plus Odonata and Belostomatidae, both aquatic insects, were the main consumed food items, which matches our hypothesis that the species would have a more aquatic diet and niche. Even with limited sampling, the results were similar to those of previous studies in coastal limnetic environments (Martínez, 2010; Ruiz-Guerra & Echeverry-Galvis, 2019). Another study at the same area demonstrated similar results, as snowy egrets tended to use limnetic environments more than other heron and egret species (Gianuca et al., 2010). Fishes and crustaceans are also important prey in a previous study in the area (Gianuca et al., 2010) as well as in the upper Paraná River floodplain (Dias et al., 2025).

Snowy egrets in our study had greater assimilation of limnetic fish, showing little variation in $\delta^{13}C$ and $\delta^{15}N$ values in blood. These results match our hypothesis of a more restrictive niche, which demonstrates that snowy egrets forage in areas near colonies rather than on marine beaches a few kilometers away. They are capital breeders, as shown by stable isotope values in eggs in a Colorado River colony in Mexico (Herzka et al., 2013). The specialist habitat of the snowy egret led to a restrict use of resources, when compared to the other species in our study. Regarding the overlap of the trophic niches between cattle egrets and black-crowned night herons, the consumption of common prey in terrestrial environments, such as insects and spiders, may characterize the most shared resources between the species. Even with the small sample size of the snowy egret, the presence of the insects in its diet was noted. This fact demonstrates that insects are important food items for all three heron species. Therefore, the current decline in the abundance and diversity of insects (Wagner et al., 2021) and the decrease in the abundance of the Brazilian silverside in the Lagoa dos Patos Estuary (Silva et al., 2021) point toward a reduction in key prey for egrets and herons, potentially influencing the whole island ecosystem. The black-crowned night heron also had a high isotopic niche overlap with the snowy egret (100%), followed by overlap with the cattle egret's niche (73.8%), which can be explained by the assimilation of varied sources, such as fish species, in comparison to other ardeids. This generalist feeding habit had led to a broader niche and resulting in high overlap with the other species. Herons and egrets that breed in sympatry may show a distinction in at least one of the niche dimensions (temporal, spatial, or trophic) during the reproductive period, which allows

for coexistence (Ye et al., 2021), as confirmed in our study.

Conclusion

Results showed that cattle egrets, snowy egrets, and black-crowned night herons share a range of upper-level prey taxa, yet differed in prey species assimilated. Although these species forage in distinct habitats from one another, they share prey species, resulting in trophic and isotopic niche overlaps. Therefore, the differences in prey consumed and assimilated and the exploration of distinct foraging sites at different periods of the day seem to allow the sympatric coexistence of the species.

The present study is the first to compare, with conventional and SIA methods, the diet and investigate resource partitioning among three ardeid species (*Bubulcus ibis*, *Egretta thula* and *Nycticorax nycticorax*) breeding at Lagoa dos Patos area. Consequently, it is important to obtain more in-depth information, especially about trophic ecology, as we know that herons, egrets, and ibises are important aquatic-terrestrial carriers of matter and nutrients (Caseiro-Silva et al., 2023) and environmental sentinels (Barreto et al., 2025). Additionally, Lagoa dos Patos is an important site for a range of waterbird species (Gianuca et al., 2010; Dias et al., 2017), emphasizing the importance of collecting in situ ecological information. Further understanding of the consumer-prey relationships, movements between environments, and the role of waterbirds in the energy and nutrient flow in food webs is needed. Our study demonstrated that sympatric species can have a trophic plasticity, being highly adaptable to different conditions and resource availability, sharing foraging areas with their conspecifics, indicating important and complex ecological interactions during the breeding season.

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Data availability Enquiries about data availability should be directed to the authors.

Declarations

Conflict of interest The authors have not disclosed any competing interests.

Ethical and sampling approval This study was approved by ICMBio/SISBIO (sampling permit No. 72947-1) and the Ethics Committee on Animal Use (CEUA-FURG, Certificate No. P028/2020).

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