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American Oystercatcher benefits from a heterogeneous landscape to breed in an urbanized area in southern Brazil

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Abstract

Urbanization is a major form of landscape transformation that often results in habitat degradation and loss for birds. However, effects on avian populations are trait- and context-dependent, and persistence at urban patches is likely to be a function of habitat availability at the landscape scale. Here, we aimed to assess the breeding performance and foraging ecology of a widespread shorebird, the American Oystercatcher *Haematopus palliatus*, during the 2017–2018 and 2018–2019 breeding seasons at a small urban beach surrounded by a heterogeneous landscape in southern Brazil. Twelve pairs were able to breed consistently and successfully fledge offspring in 20% of nesting attempts at the urban site, with overall productivity of 0.37 fledglings per pair. Food remains collected within seven successful nesting territories and stable isotope analysis in blood samples of adults and chicks indicated that oystercatchers relied on invertebrates from both sandy beaches and rocky shores as food resources. Furthermore, eight out of 21 color-marked individuals from the urban beach were consistently recorded using an insular marine protected area ~ 2 km offshore, revealing a connection between unprotected and protected habitat patches. Although oystercatchers had to perform multiple foraging trips in order to collect food, the ability to explore different environments in the landscape may be critical in the region, especially with human disturbance at its peak on beaches during the summer. Our findings suggest that shorebirds breeding in urban areas may rely on heterogeneous landscapes, where distinct and protected habitat patches can provide complementary resources that allow breeding successfully.

Keywords Breeding performance · Foraging ecology · Habitat connectivity · *Haematopus palliatus* · Shorebirds · Stable isotopes

Introduction

Human population size is rapidly increasing and transforming natural ecosystems worldwide through urban development (Marzluff 2001; Murgui and Hedblom 2017). Urbanization is an extreme form of landscape transformation and a major cause of habitat degradation and loss for many bird species and ecosystems, although individuals may find ways to persist in these altered environments (González-Oreja 2011). Several studies have demonstrated that effects of urbanization on avian populations are complex and depend on species' traits and environmental variables (e.g. González-Oreja 2011; Jokimäki et al. 2016). Many wild birds decline or are locally extinct due to their intolerance to human disturbance and/or dependence on specific, preserved habitats to nest and feed (Bonier et al. 2007). However, some species may tolerate and even benefit from urban environments and establish dense populations in urban areas due to ameliorated climate and abundant anthropogenic resources (Yorio et al. 1998; Marzluff 2001; Caron-

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Beaudoin et al. 2013; Kettel et al. 2019). Variable responses of bird species to urbanization are often associated to the capability of adjusting behavior, ecology and physiology in response to novel conditions, with ecological generalists having advantage over specialists (Bonier et al. 2007; Méndez et al. 2020). Nevertheless, birds respond to habitat features through a range of spatial scales, and persistence in an urban patch may depend on broad landscape characteristics rather than solely on the patch itself (Bolger 2001; Hostetler 2001). For instance, heterogeneity at the landscape scale may benefit local persistence, as distinct habitat patches may differ in prey abundance, predation risk and type and extent of human-induced disturbance (Bolger 2001; Evens et al. 2018).

The impacts of human development on coastal wildlife deserves especial concern, given that over 40% of the world's population and 65% of the largest cities (i.e. > 5 million people) are located within the coastal zone (Martínez et al. 2007; McGranahan et al. 2007; Firth et al. 2016). Coastal sandy beaches are important habitats for birds but are under intense pressure from increasing coastal development and human disturbance (Defeo et al. 2009; Meager et al. 2012). Many shorebird species are sensitive to these threats once they use sandy shores as nesting, roosting and foraging habitats and rely on intertidal invertebrates as irreplaceable food resources (Schlacher et al. 2016, 2017). Human activities on beaches reduce functional habitats and may negatively influence the reproductive fitness of beach-nesting birds through direct mortality (Sabine et al. 2006), or indirectly, through reduced foraging (Defeo et al. 2009; Martín et al. 2015), prey availability (Schlacher et al. 2016) and nest attendance, exposing eggs and chicks to harsh weather, predation and starvation (Boyle and Samson 1985). Furthermore, chronic disturbance may constrain spatial use and cause shorebird numbers to decline on sandy beaches (Burger and Niles 2013; Cestari 2015; Martín et al. 2015). This may be especially harmful when feeding conditions are poor or undisturbed areas are not available at short distances (Goss-Custard et al. 2006). Nevertheless, avian species can persist in urban areas if predictable food resources are available and breeding habitat is suitable, as well as if breeding and foraging performances are not fully constrained by disturbance (Baudains and Lloyd 2007; Cardilini et al. 2013; Méndez et al. 2020).

Oystercatchers (Haematopodidae) are interesting models when investigating the shorebird ability to adapt to urban environments as well as the role of key habitats in that process, once they are widespread, long-living animals, supposedly restrict in habitat use and sensitive to human disturbance (American Oystercatcher Working Group et al. 2012). Ecological plasticity has been observed in Eurasian Oystercatchers (*Haematopus ostralegus*) due to the recent colonization of inland human-modified environments (van de Pol et al. 2014), diverse feeding strategies among individuals (van der Kolk et al. 2020) and outstanding reports on bread consumption and successful roof nesting in urban areas (Duncan et al. 2001; van Dijk 2014). A less studied relative, the American Oystercatcher (*H. palliatus*, hereafter "oystercatcher") occurs strictly along the coasts from North to South America, moreover breeding and foraging mainly on sandy beach environments, where it is known to use bivalves and other benthic invertebrates as food resources (Hockey 1996; García et al. 2010). Distinct coastal habitats may be alternatively used, such as mudflats, salt marshes and, less commonly, rocky shores (Hockey 1996; American Oystercatcher Working Group et al. 2012). Intense territorial defense, biparental care and semiprecocial chicks indicate that adult oystercatchers require appropriate food availability near the nesting site for the long breeding period (~5 months; Schulte and Simons 2015). As a result, high quality breeding areas are associated with the presence of adjacent foraging habitat (Nol 1989; Schulte and Simons 2015). Nonetheless, oystercatcher species may nest successfully in territories without local food resources if availability of profitable prey in distant foraging areas compensates the cost of multiple foraging trips (Nol 1989; Ens et al. 1992). On urban beaches, disturbance locally constrains the foraging performance, so individuals may depend on maintaining links between suitable foraging areas in order to meet their energetic requirements, especially during the breeding season.

The southernmost region of the Brazilian coastline is recognized as a key-site for the conservation of the oystercatcher in the Southern Hemisphere (Clay et al. 2014). The coast is characterized by dissipative, microtidal, wave-exposed and continuous sandy beaches linked to dunes and only interrupted by few estuaries of coastal lagoons (Amaral et al. 1999; Esteves et al. 2003). This extensive shore holds intertidal benthic invertebrates that support a shorebird assemblage composed by resident and migratory species (Gianuca 1983; Vooren and Chiaradia 1990; Scherer and Petry 2012). However, this coastal zone has dramatically changed in the last decades due to the increase of human occupation (Esteves et al. 2003; SEPLAG 2020). In addition, developed coastal cities face an average population growth of about 140% during summer as a result of tourism and recreational use of beaches (Zuanazzi and Bartels 2016; SEPLAG 2020), which degrades the habitat of coastal organisms, including resident shorebirds during the breeding season (Leal et al. 2013; Schlacher et al. 2016; Bom and Colling 2020). Nevertheless, the coast surrounding Praia Grande (Torres city), a small intensely developed urban beach (Cristiano et al. 2016), is a unique region along the southernmost Brazilian coastline that incorporates sandy beaches and dunes, rocky shores and a marine protected island nearby (Esteves et al. 2003; Engel et al. 2014). This heterogeneous landscape, in comparison to the continuous south and northward sandy coastline, may provide additional food resources and alternative habitats for shorebirds facing human pressure on beaches.

The present study aimed to investigate the breeding and foraging ecology of oystercatchers nesting on Praia Grande, southern Brazil. A nest monitoring was carried out during two consecutive breeding seasons to assess the breeding success and phenology. Food remains delivered to chicks and stable isotope analysis (SIA) were used to infer the diet and important foraging habitats for oystercatchers during the breeding period. In addition, a mark-resight program was initiated in order to understand movements between urban and protected habitat patches. Due to the intense human disturbance on the beach, mainly during the breeding season, we expected oystercatchers to have low breeding success at the urban site, and to rely on different habitats available in the landscape for foraging while breeding.

Materials and methods

Study area

The study was carried out in Praia Grande (29°20'S; 49°43'W), the main beach of the city of Torres, southern Brazil. Torres is one of the largest cities in the region with around 40,000 inhabitants (IBGE 2020). Praia Grande beach receives intense human pressure from beach recreation (Fig. S1 in Online Resource 1), especially from December to February, when summer population in Torres increases to more than double the number of year-round residents (Zuanazzi and Bartels 2016). The beach is ~1.7 km long and contains an area (~20 ha) of vegetated sandy dunes of ~1.5 km long and up to ~150 m of width (Linhares et al. 2021), bordered by extensive urban infrastructure (Fig. S2 and S3 in Online Resource 1). The dunes are crossed by eight footpaths that lead to the beach, from which one is a boardwalk.

The coast near Praia Grande is composed by sandy beaches and rocky shores (Fig. S4 in Online Resource 1), including a marine protected island: the Wildlife Refuge of Ilha dos Lobos (Fig. 1; Fig. S5 in Online Resource 1). Ilha dos Lobos is a small rocky island with an area of 16,970 m^2, located about 2 km off Praia Grande, and it protects migratory fur seals and sea lions, as well as seabirds and shorebirds (Engel et al. 2014; Procksch et al. 2020; Rosso 2020). Landing and resource exploitation are forbidden on the island, in accordance with the IUCN Category III of protected areas (Day et al. 2019).

Monitoring of breeding activities

Active search for breeding oystercatchers and nests was carried out on Praia Grande from July 2017 to February 2019, along two full breeding seasons (2017–2018 and 2018–2019). Surveys ($n = 51$) transpired weekly from July 2017 to January 2018, and then fortnightly from February 2018 to February 2019, but for three months (June, July and October 2018) there was a single fieldwork day each month. Surveys focused on the dunes and in the 1.5 km long beach section, because this area provides a typical environment for nesting oystercatchers in southern Brazil (Canabarro and Fedrizzi 2010; Linhares et al. 2021). In each survey (3 to 6 h of duration depending on the timing of the breeding season), breeding pair counts and monitoring of nests and chicks were performed subsequently, on foot, following a zigzag path on the dunes. Behavioral cues – such as alarm calls, false incubation or incubation, and aggressive flights towards the observer – were used in order to identify and count breeding individuals, as well as searching for potential nest-sites (Hostetter et al. 2015; Schulte and Simons 2015). The highest abundance of breeding pairs recorded in at least three surveys was used to infer the number of pairs breeding in the area (e.g. Davis et al. 2001). Breeding pair abundance per km of coastline (hereafter "encounter rate") was calculated considering the length of the monitored coastline (i.e. 1.5 km; e.g. McGowan et al. 2005; Clay et al. 2014; Vega-Ruiz et al. 2019).

Whenever a nest was found, clutch size was recorded and the nest-site was monitored over time to confirm breeding success. Hatching success was confirmed when at least one egg from the clutch hatched and the chick was found (Lauro and Burger 1989; Sabine et al. 2006). Fledging success was defined when at least one chick was observed in sustained flight (Davis et al. 2001; Traut et al. 2006; Virzi et al. 2016). Hatching and fledging success were calculated as a proportion of the total number of nests. The breeding phenology was characterized monthly considering the total number of active nests, chicks and juveniles (i.e. post-fledge chicks), as well as the mean abundance of breeding pairs recorded. In addition, notes on potential predators and human disturbance were recorded.

Marking and blood sampling

Oystercatchers were captured at night by using LED flashlights to disorient birds and handle nets to capture them. Whole blood samples were collected from the tarsal vein with syringe and needle and stored in plastic tubes with 70% ethanol for later SIA. Samples were only taken from chicks once they were at least three weeks old, considering the half-life of $\delta^{13}C$ and $\delta^{15}N$ in the blood (two weeks in shorebirds; Ogden et al. 2004), avoiding value build up on egg nutrients. Each bird received an individually numbered metal band and a unique combination of color plastic rings in their tarsus, which allows remote individual identification.

Analysis of food remains

During the chick-rearing period, adults of oystercatcher species provision chicks with food, accumulating hard remains of consumed prey (e.g. empty shells of mollusks) in the

Fig. 1 Satellite image showing a section of Torres coastline, southern Brazil, highlighting Praia Grande beach, where nests of the American Oystercatcher (*Haematopus palliatus*) were monitored, Ilha dos Lobos island, the Mampituba inlet and (in black) some of the rocky outcrops that exist in the region

territories where chicks are fed (hereafter "nesting territories"; Hockey and Underhill 1984). Nesting territories were identified on the dunes of Praia Grande by observing breeding activities, such as territorial defense, movement of chicks and presence of food remains. Prey remains were collected from the nesting territories which fledged chicks during the study period ($n = 7$ nests), from hatching and then fortnightly until the end of the chick-rearing period. Therefore, three to six samples of prey remains were collected from each nesting territory depending on the length of the chick-rearing period, for a total of 29 samples. Prior to the collections performed in the nesting territories, a large effort was placed in July 2017 (i.e. first month of fieldwork) to remove all potential food remains from the dunes area. This removal delimited an unbiased baseline for new material to accumulate along the study period, and thus was not considered in our analyses.

All food remains were stored in plastic bags for later identification and quantification at the laboratory. Intact shells were measured with dial calipers to determine prey sizes. For each food item, the following parameters were calculated: frequency of occurrence (FO, i.e. the number of samples containing the food item); relative frequency of occurrence (FO%, i.e. FO as a proportion of all samples analyzed); numerical contribution (N, i.e. number of each food item in the pooled samples); relative numerical contribution (N%, i.e. N as a percentage of the food item in the pooled samples).

Stable isotope analysis

Individuals of prey species previously identified in food remains were collected in or near Praia Grande beach in 2018 and 2019 for SIA. In the laboratory, whole bodies of crustacean prey and muscle samples of mollusks were used. Prey samples were washed in a Soxhlet extractor during a 6 h cycle to remove lipids, using a 2:1 chloroform:methanol solution as solvent. Prey samples and the oystercatcher blood were freeze-dried and grounded, and subsamples of ~0.7 mg were placed into tin capsules for analysis using isotope ratio mass spectrometry (measurement precision of 0.1‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$) at the *Centro Integrado de Análises* of the

Universidade Federal do Rio Grande (CIA-FURG, Brazil). Differences between sample ratios and the international reference standards (Vienna Pee Dee Belemnite limestone for carbon, and atmospheric air for nitrogen) were expressed in δ notation as parts per thousand (‰; Bond and Hobson 2012):

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

where $\mathrm{R} = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ or ${}^{15}\mathrm{N}/{}^{14}\mathrm{N}$. Carbon and nitrogen isotopic ratios were used to estimate the isotopic niche of oystercatchers through the SIBER package in R (Jackson et al. 2011). For this, standard ellipse areas (‰^{2}) corrected for small sample sizes (SEAc) were estimated for both chicks and adults, as well as the overlap percentage between ellipses. Furthermore, the contribution of each food item in the diet of chicks and adults was estimated using δ^{13}C and δ^{15}N values to generate Bayesian mixing models in R using the simmr package (Parnell and Inger 2016). Trophic discrimination factors selected in the models were 0.2 ± 0.4‰ for δ^{13}C and 2.7 ± 0.4‰ for δ^{15}N, as estimated and used in a field study with the African Black Oystercatcher (*H. moquini*) in South Africa (Kohler et al. 2011). Isotopic ratios of the five food items with the highest abundances in the food remain analysis (see Results) were used as sources in the model, including three bivalves (*Amarilladesma mactroides*, *Donax hanleyanus*, *Perna perna*), one gastropod (*Olivancillaria vesica auricularia*) and one crustacean (*Emerita brasiliensis*). Three filter-feeding species from sandy beaches (*A. mactroides*, *D. hanleyanus* and *E. brasiliensis*) had similar isotopic values and were pooled for the analysis, as suggested by Phillips et al. (2005).

Island sightings

To investigate if oystercatchers breeding in Praia Grande use a nearby and protected marine island, we performed on-board excursions to the surrounding waters (< 200 m) of Ilha dos Lobos. A total of 17 surveys were performed between January 2018 and March 2019 (at least once a month) with a touristic vessel or a motorboat, which navigated around the island for up to 20 min. Birds spotted on the island were recorded using digital cameras with 300–500 mm telemeter lens. Images were then analyzed to quantify the total number of oystercatchers and identify color-ringed individuals.

Results

Breeding phenology and success

We found 35 nests (n = 20 in 2017–2018, n = 15 in 2018–2019), most in the sandy dunes area. A single nest was recorded on the beachfront. The breeding season lasted eight months, from July (first nesting activity) to February (last juvenile recorded), with peak numbers of nests, chicks and breeding pairs in November (Fig. 2). Although few breeding pairs were still engaged in chick-rearing and incubation in December and January (both seasons), flocks of up to 12 individuals, including color-marked adults and juveniles, were recorded on dunes just before their departure from the breeding area in February. During the non-breeding period, which extended from March to June, only pairs with no breeding behavior were recorded.

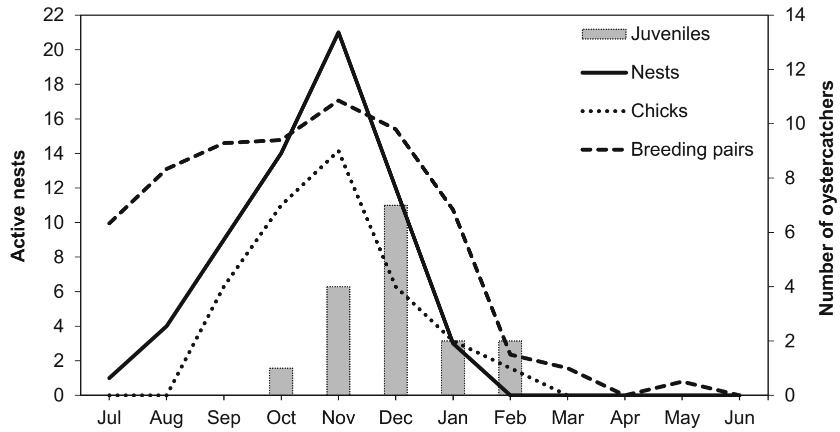
Peak counts detected 12 pairs using Praia Grande as a breeding site in each season, resulting in an encounter rate of 8 pairs/km. Overall hatching success was 42.9% and fledging success 20% (Table 1). In the 2017–2018 breeding season, one chick fledged per clutch, while in the 2018–2019 two clutches fledged two chicks each. The clutch size mode was two eggs (mean = 1.8 ± 0.5), with two eggs being recorded in 71.4% of the nests, followed by one (22.9%) and three eggs (5.7%). It was estimated that at least six (30%) nests from the 2017–2018 season and four (26.7%) from the 2018–2019 season were renesting (i.e. nest at the same place, after success or failure of a previous nest by presumably the same pair), which includes both the second (70%) and third (30%) nesting attempts from the same breeding pair within the breeding season.

During nest monitoring, the Southern Crested Caracara *Caracara plancus*, Chimango Caracara *Milvago chimango* and the Black Vulture *Coragyps atratus* were recorded as potential native nest predators, frequently surveying the area alone or in pairs and occasionally being chased away by oystercatchers and Southern Lapwings *Vanellus chilensis*. Burrowing Owls *Athene cunicularia* nest on the dunes but no interaction with oystercatchers was recorded. Human activities were intense on the beachfront especially in summer and holidays, flushing foraging oystercatchers. Even though people access the beach through the dunes, it is hardly used for other purposes. Free roaming dogs occasionally wander the area and chased oystercatchers on both the beachfront and dunes.

Dietary analysis

A total of 1539 prey from six species of marine invertebrates were counted in the samples obtained from the seven successful nesting territories during the study period. Prey belonged to three taxonomic Classes: Bivalvia (n = 1075), Gastropoda (n = 289) and Malacostraca (n = 175; Table 2). The most consumed food item differed across the individual nesting territories and between the two breeding seasons, with *P. perna* (n = 419; 57.9%) being the most numerous species in 2017–2018 and *D. hanleyanus* (n = 433; 53.1%) in 2018–2019 (Fig. 3).

Fig. 2 Number of active nests, chicks, juveniles (total found in both seasons) and breeding pairs (count means) of the American Oystercatcher (*Haematopus palliatus*) throughout the year in Praia Grande beach, southern Brazil, during two breeding seasons (2017–2018 and 2018–2019)



Fifteen blood samples were obtained from adults (n = 10) and chicks ($n = 5$). Isotopic values ranged from −14.3 to −13.2‰ for δ^{13}C and 11.8 to 14.3‰ for δ^{15}N. Values of potential food items ranged from −14.6 to −11.8‰ for δ^{13}C and from 8.3 to 14.5‰ for δ^{15}N (Table S1 in Online Resource 1; Fig. 4). The mixing models indicated that oystercatchers relied on filter-feeding invertebrates from sandy beaches and rocky shore *P. perna* as main food resources, while assimilating less of *O. v. auricularia* (Fig. 5). Chicks presented 84% probability of consuming *P. perna* in higher proportions than adults, whereas adults had a higher probability of assimilating filter-feeding invertebrates from sandy beaches and *O. v. auricularia* in higher proportions than chicks (66.2% and 69.3%, respectively). Adults presented a higher isotopic niche (SEAc = 6.6) than chicks (SEAc = 2.0), with 22% of the Bayesian ellipse of adults overlapping with that of chicks, and 72.2% of the chicks' niche overlapping with adults (Fig. 6).

Marking and resightings

Twenty-one oystercatchers (10 adults, 11 chicks) were banded in Praia Grande along the two breeding seasons. Along 17 expeditions to Ilha dos Lobos, up to 37 oystercatchers were counted simultaneously on the island (Fig. 7). Color-marked individuals were recorded in 64.7% of the expeditions, and were undetected only when no oystercatchers were sighted on the island. A total of eight marked individuals were sighted in the marine protected area, corresponding to 50% ($n = 5$) of the adults and 27.3% ($n = 3$) of the chicks marked during the study period. Each individual was sighted from one to seven times, comprising 21 separate records. Three juveniles (one from the 2017–2018 and two from the 2018–2019 season) were recorded on the island a few weeks after the fledging period, between January and March, one being recorded on three consecutive expeditions.

Table 1 Reproductive success of the American Oystercatcher (*Haematopus palliatus*) in Praia Grande beach, southern Brazil, during the 2017–2018 and 2018–2019 breeding seasons

Breeding season	Active nests	No. of nests that hatched eggs (%)	No. of nests that fledged chicks (%)	% of hatched clutches that fledged chicks	No. of fledged chicks	No. of fledged chicks per breeding pair
2017–2018	20	9 (45.0)	3 (15.0)	33.3	3	0.25
2018–2019	15	6 (40.0)	4 (26.7)	66.7	6	0.50
Combined	35	15 (42.9)	7 (20.0)	46.7	9	0.37

Table 2 Diet of American Oystercatchers (*Haematopus palliatus*) in Praia Grande beach, southern Brazil, based on the pooled samples of food remains collected from seven nesting territories during the 2017–2018 and the 2018–2019 breeding seasons

Food items	Frequency of occurrence		Contribution by number		Mean length ± 1 standard deviation (mm)	Min – max length (mm)
	FO	FO%	N	N%		
Crustacea: Malacostraca	–	–	175	11.4	–	–
Emerita brasiliensis [a]	15	51.7	175	11.4	~30.0±NA	–
Mollusca: Bivalvia	–	–	1075	69.8	–	–
Amarilladesma mactroides [a]	9	31	67	4.3	56.2±7.1	45.3–79.2
Donax hanleyanus [a]	26	89.6	489	31.8	26.2±2.4	17.5–31.3
Perna perna [b]	22	75.9	519	33.7	50.1±7.9	24.8–71.8
Mollusca: Gastropoda	24	82.8	289	18.8	–	–
Olivancillaria vesica auricularia [a]	24	82.8	277	18.0	34.2±2.8	20.1–48.0
Stramonita haemastoma [b]	5	17.2	12	0.8	32.1±5.1	24.5–40.1
Total	29		1539			

[a] Food items from sandy beaches; [b] Food items from rocky shores

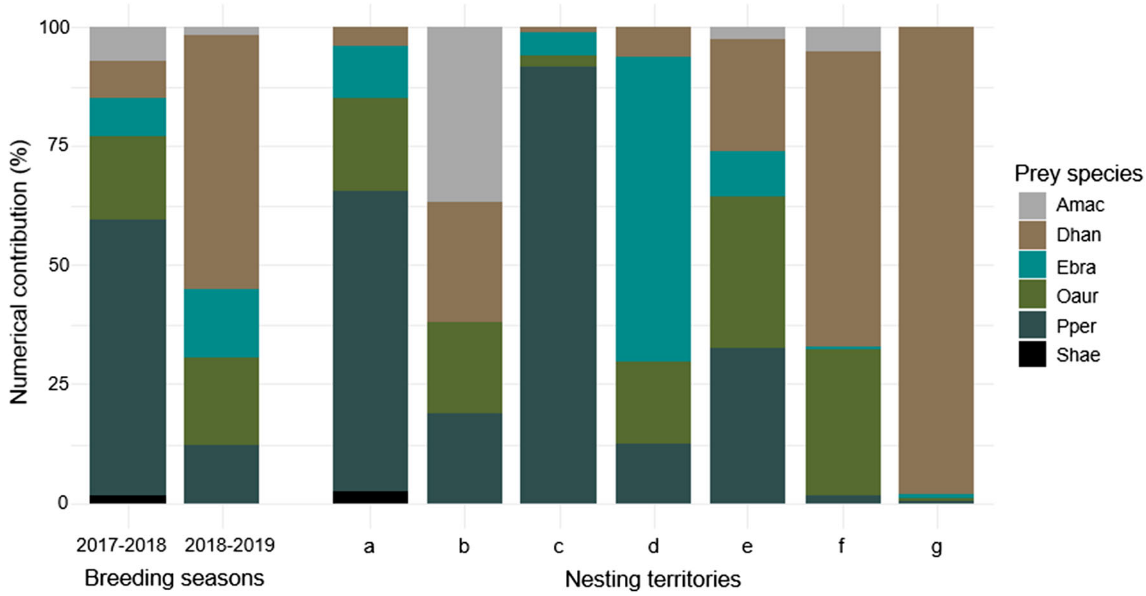


Fig. 3 Relative numerical contribution (N%) of prey species to the diet of American Oystercatchers (*Haematopus palliatus*), inferred through food remains collected from nesting territories during two breeding seasons (2017–2019) in Praia Grande beach, southern Brazil. Graphic representations are given for the pooled samples of each breeding season and for individual nesting territories within the 2017–2018 (a, b and c) and 2018–2019 (d, e, f and g) breeding seasons. Amac = *Amarilladesma mactroides*, Dhan = *Donax hanleyanus*, Ebra = *Emerita brasiliensis*, Oaur = *Olivancillaria vesica auricularia*, Pper = *Perna perna*, Shae = *Stramonita haemastoma*

Discussion

Main findings demonstrated that oystercatchers, although sensitive to coastal development and human disturbance, were able to breed consistently and successfully at this urban site in southern Brazil. Furthermore, diet assessed by food remains and SIA along with the sightings of color-marked individuals showed that birds relied on prey gathered on sandy beaches, rocky shores and a nearshore protected island during the breeding period. These findings reveal that oystercatchers are able to explore different habitat elements in the landscape in order to maintain breeding activities at an urbanized patch, thus benefiting from habitat heterogeneity.

Urban effects on breeding performance

Human disturbance is highly expected to reduce the reproductive fitness of beach-nesting birds, causing direct and indirect nest failure (Sabine et al. 2006; Defeo et al. 2009; Schlacher et al. 2016). However, the 20% fledging success recorded was higher than what was reported on oystercatchers in another study conducted in southern Brazil (0%; Canabarro and Fedrizzi 2010), on two protected barrier islands in North Carolina (USA) from 1997 to 1999 (2–7%; Davis et al. 2001) and in the same habitat in Virginia (USA) in 1979 and 1984 (14.3 and 0%; Nol 1989), but lower than 1982 and 1983 (41.5 and 48.8%; Nol 1989). Moreover, the encounter rate of 8 breeding pairs per km was relatively high in comparison to estimates in other sites throughout the species distribution: a sandy beach in southern Brazil (1.1 pairs/km; Clay et al. 2014, data from Canabarro and Fedrizzi 2010), a barrier island in North Carolina (0.6 pairs/km; McGowan et al. 2005), and across most habitats in Mexican islands (0 to ~13 pairs/km; Vega-Ruiz et al. 2019). Although the breeding parameters of oystercatchers reported on the studies mentioned above are variable and obtained in diverse environmental situations, the persistence of several pairs breeding regularly and successfully on this small urban beach under intense human pressure in southern Brazil is remarkable. Furthermore, demographic modeling suggested that a few years with high reproductive success are enough to ensure population viability for oystercatchers (Schulte 2012; Schulte and Simons 2016). Although our data is based on only two breeding seasons and lacks estimates of adult and chick survival, the estimate of 0.50 fledglings per pair in the 2018–2019 season is higher than the projected baseline to sustain a stable population (= 0.39 fledglings per pair; Schulte 2012).

Given that shorebirds usually do not tolerate human approximation to less than several tens of meters (Glover et al. 2011; Cestari 2015), the intense recreational use of Praia Grande would be expected to reduce oystercatcher numbers by constraining beachfront use during the nesting season (Burger and Niles 2013; Martín et al. 2015). Nevertheless, breeding density and success are often associated with habitat suitability, and beach-nesting birds may exhibit a clumped dispersion where food availability is high (Schlacher et al.

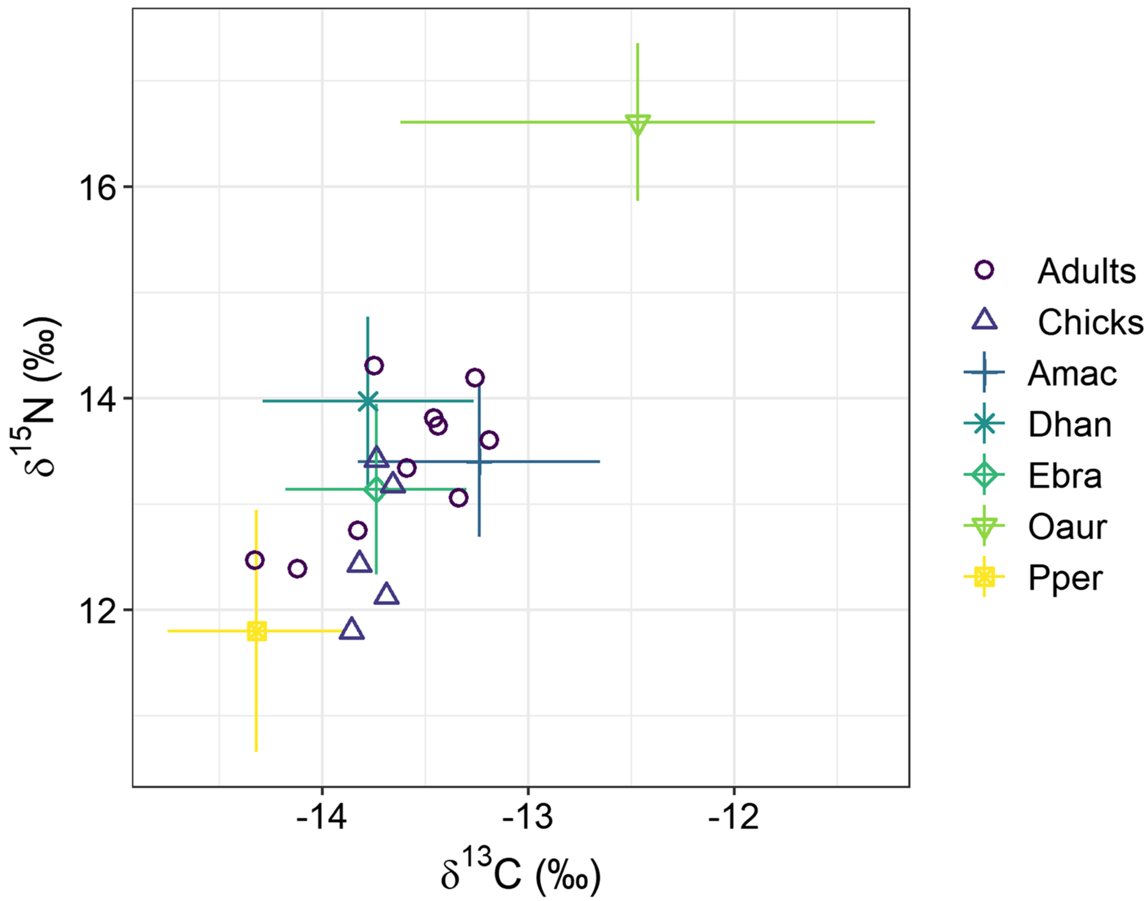


Fig. 4 Isospace with δ^{15}N and δ^{13}C (in ‰) in the whole blood of adult and chick American Oystercatchers (*Haematopus palliatus*) from Praia Grande beach, southern Brazil, and potential food items (marine invertebrates). Source values were corrected for a consumer-diet discrimination factor (2.7 ± 0.4‰ for δ^{15}N and 0.2 ± 0.4‰ for δ^{13}C). Prey species Amac, Dhan and Ebra were later combined for the analysis due to similar isotopic values and ecology. Abbreviations are given in Fig. 3

2016). Thus, the breeding performance reported here must be related to the presence of relatively wide vegetated dunes (~150 m) providing shelter for nesting (Linhares et al. 2021) and roosting, as well as the availability of prey in the less-disturbed rocky marine environments nearby, including a marine protected area, in addition to the regular beachfront habitat.

Furthermore, shorebirds may habituate to the disturbance stimuli to some extent if human presence is mostly non-threatening and/or if urbanization excludes important nest predators (Stillman and Goss-Custard 2002; Baudains and Lloyd 2007; Cardilini et al. 2013). The finding that the studied oystercatchers bred in a moderate abundance and successfully raised offspring suggests that these birds may be experiencing some level of habituation to disturbance. In Praia Grande, human presence is intense on the beach but is not widespread on dunes, the main nesting habitat. Furthermore, apart from records of some potential avian nest predators, free roaming dogs were only eventually recorded during the study period, and we assume that the surrounding urbanization prevent the access of other potential native mammalian predators, such as the Crab-eating Fox *Cerdocyon thous* and the Southern Tiger Cat *Leopardus guttulus* that occur in a coastal protected area distant about 3 km away (Parque Estadual de Itapeva; SEMA 2006). Moreover, the nesting of the Southern Lapwing – an aggressive territorial shorebird, highly tolerant to urbanized environments (Walters 1990; Sick 1997) – during the same period in the sandy dunes (Oliveira 2018) may increase surveillance and nest-site protection for both species, as they were recorded attacking raptors simultaneously (B.A. Linhares pers. obs.).

Nevertheless, urbanization may have various effects on breeding parameters of avian populations, including shifts in phenology. The peak of oystercatchers nesting activity in mid spring in the study area is similar to previous studies in temperate and subtropical regions in both hemispheres (Nol et al. 1984; Nol and Humphrey 1994; Barbieri and Delchiaro 2009; Bachmann and Darrieu 2010; Canabarro and Fedrizzi 2010).

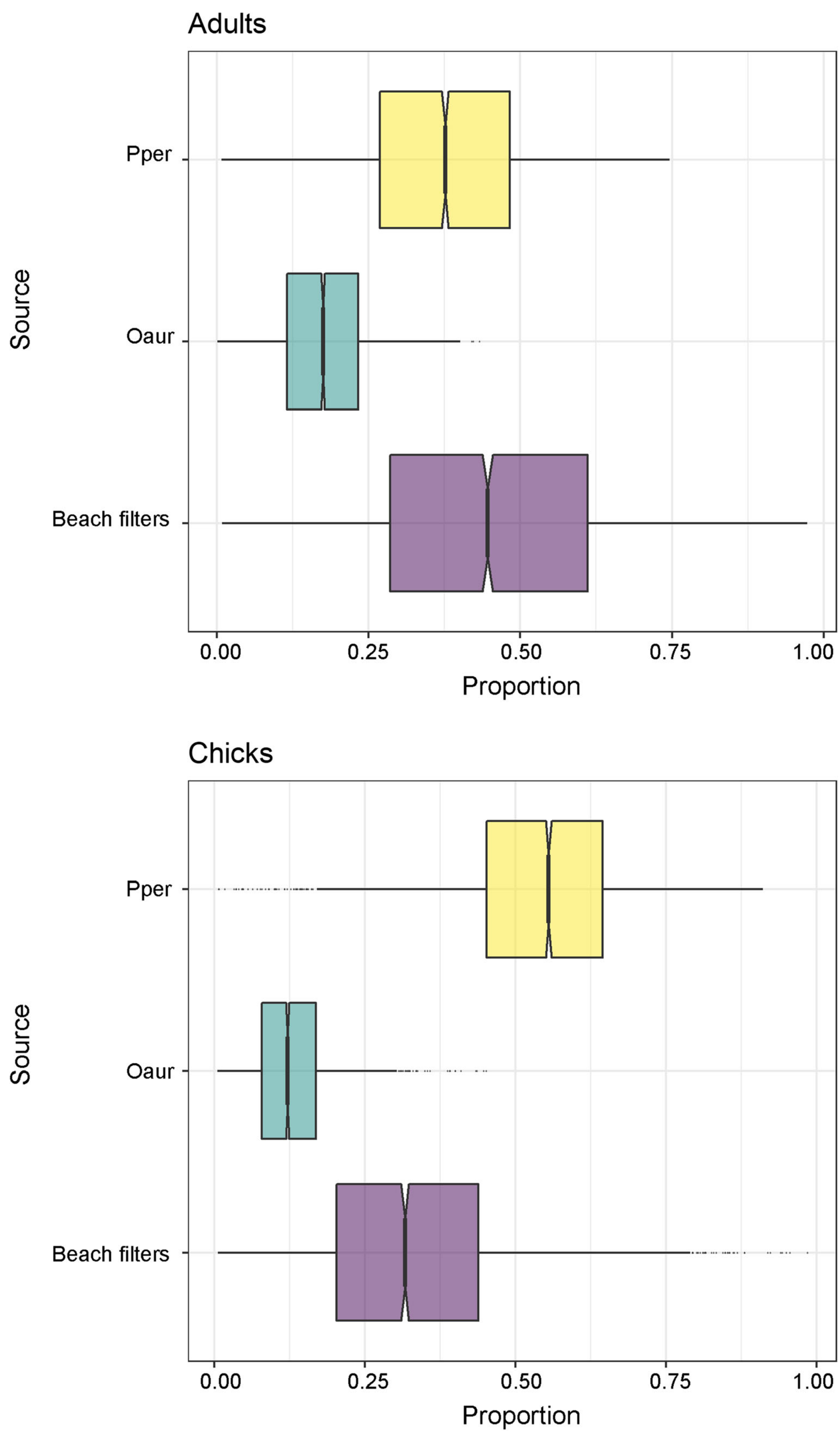


Fig. 5 Output of Bayesian stable isotope mixing models representing the estimated contributions (mean, 25% and 75% percentiles) of different prey sources for the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic values in the blood of American Oystercatchers (chicks and adults) from Praia Grande beach, southern Brazil. 'Pper' and 'Oaur' are prey species, while 'Beach filters' is a source combining three filter-feeding intertidal invertebrates from sandy beaches (Amac, Dhan and Ebra). Abbreviations are given in Fig. 3

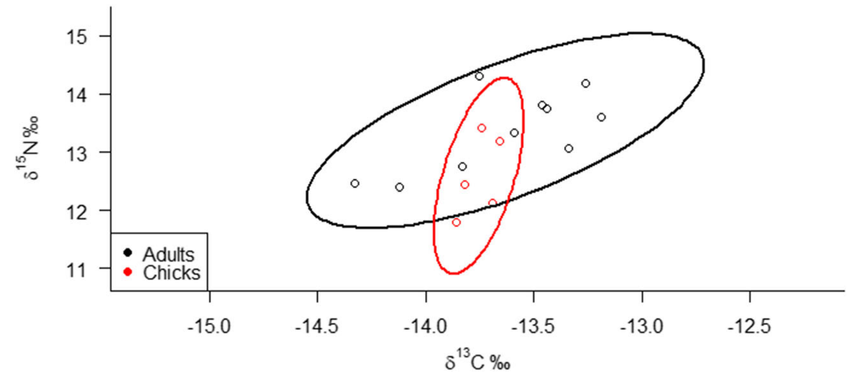


Fig. 6 Standard Bayesian ellipses generated with carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopic values from the whole blood of adult and chick American Oystercatchers (*Haematopus palliatus*) from Praia Grande beach, southern Brazil. Ellipses comprise 95% of the data

However, laying initiation dates are rarely reported in the winter (American Oystercatcher Working Group et al. 2012), when both nests and chicks were recorded at Praia Grande. An advanced breeding period could be a response to the environmental stimuli in this urbanized beach. There are vast evidences that some bird species experience an earlier onset of breeding in urban areas, what is attributed to several potential causes, such as light pollution, warmer microclimate, increased food availability and higher social stimulation (Partecke et al. 2004, 2005; Dominoni et al. 2013). In addition, for a beach-nesting species, breeding earlier might present more opportunities of renesting in case of nest failure (Morrison et al. 2019) and be an advantage when avoiding the peak of human disturbance and beach recreation during summer. Indeed, we recorded few birds continuing breeding activities in early summer, when post-season flocks were recorded, which indicates that the majority of birds from Praia Grande were already in their non-breeding period. Although the causes of the advanced breeding period observed here are not conclusive and deserve further investigation, this finding broadly suggests that urbanization may affect the phenology of shorebirds nesting on beach environments.

Foraging ecology and use of a nearby protected area

Food remains and SIA, the later apparently used for the first time in American Oystercatchers, confirmed its molluscivorous specialization although also having consumed other taxa, relying on a few marine invertebrates found on both sandy beaches and rocky shores as main food resources. These findings highlight that distinct habitat patches available in the landscape may provide important food resources for oystercatchers during the nesting season in urban areas.

Food items from sandy beaches compose the bulk biomass in intertidal marine habitats in southern Brazil (i.e. *E. brasiliensis*, *D. hanleyanus* and *A. mactroides*), with the exception of the less abundant predator *O. v. auricularia* (Gianuca 1983; Neves and Bemvenuti 2006). However,

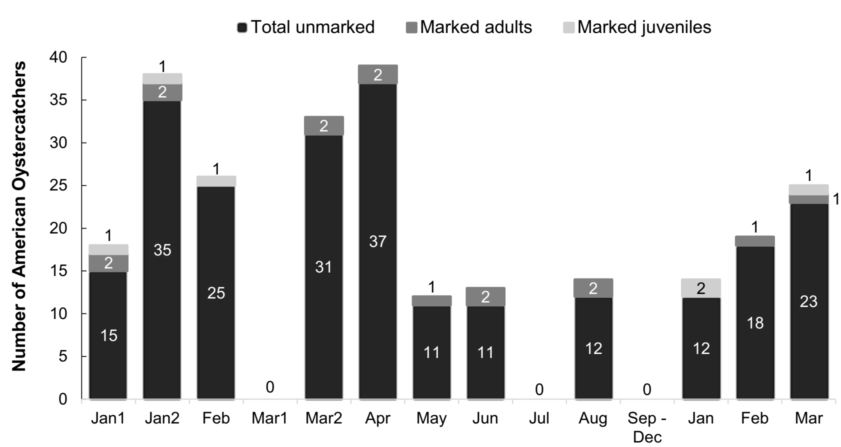


Fig. 7 Numbers of American Oystercatchers (*Haematopus palliatus*) recorded during on-board expeditions to the surrounding waters of the marine protected area of Ilha dos Lobos, southern Brazil, between January/2018 and March/2019. Marked birds from Praia Grande beach were identified by a unique combination of color plastic rings. When more than one expedition was performed in a given month, a second bar was added. Months from September to December/2018 were grouped in the graphic, since no American Oystercatcher was recorded

foraging on rocky shores was critical during the chick-rearing period, given that the large-sized (~50 mm) *P. perna* had the highest numerical contribution detected in food remains, whereas the much smaller *D. hanleyanus* (~26 mm) was the most abundant prey from sandy beaches. Although remains of potential soft-bodied prey (e.g. worms and small crustaceans) are hardly detected on nesting territories, food remains probably reflect the bulk of chicks diet, given that oystercatchers are mollusk-feeding specialists and tend to provide large prey to their offspring (Hockey and Underhill 1984; Hockey 1996). In addition, SIA suggested that adults fed on resources from sandy beaches in higher proportions, whereas *P. perna* appeared to represent a larger proportion in chicks' diet. Nonetheless, mixing models were based on small sample size for chicks and may be influenced by a potential unequal isotopic fractionation in the blood of chicks and adults derived from different metabolism (Bearhop et al. 2000). Despite these limitations, the wider isotopic niche breadth found in adults suggests that they may have a broader diet, while chicks are fed with a more restricted set of resources. A possible scenario may be that adults feed opportunistically for themselves in different habitat patches while searching for specific, predictable and high-quality prey (i.e. large *P. perna*) to provision chicks.

Despite the occurrence of beach invertebrates in the intertidal area of Praia Grande, adults had to move between patches of rocky shores in the landscape in order to obtain *P. perna* to their chicks, on the few rock outcrops on the shore and on the protected island (Ilha dos Lobos), 2 km offshore. Indeed, recordings of color-marked birds indicates foraging of the breeding individuals on the island, highlighting the connection between the urban nesting site and the marine protected area. As human recreation depletes intertidal resources and constrain foraging activity of shorebirds on beaches (Meager et al. 2012; Schlacher et al. 2016; Bom and Colling 2020), this protected foraging habitat may be important for the establishment and success of oystercatchers in Praia Grande. Moreover, records of juveniles on the island during summer suggest that this protected area may also serve as a refuge for recently fledged individuals when human disturbance is intense on the beaches, providing an adequate roosting and foraging habitat. This could potentially have long-term fitness consequences, increasing the quality (e.g. body condition) and first-year survival of young birds (Lindström 1999).

Although our results suggest that rocky shore foraging is an important habit for oystercatchers, detection of *P. perna* on food remains was dominant in some nesting territories, but almost absent in others. Differences between chick diets suggest that some level of individual and/or breeding pair specialization occurs. As different food items require strikingly different foraging skills to oystercatchers, specialization is expected to reduce handling time, maximize food intake and minimize intraspecific competition (Sherry 2016). However, variations observed in the diet may also be related in part to interannual variation in prey availability on sandy and rocky shores, as most consumed food items differed between breeding seasons. Once oystercatchers are efficient in detecting patches with higher prey biomass on the environment (Schwemmer et al. 2016), there is a possibility they might switch target prey (or foraging habitat) in response to changes in food availability, as a functional response (Goss-Custard et al. 2006). Moreover, some studies have shown that natural events can modify the coastal environment used by oystercatchers, changing accessibility to foraging sites and influencing their reproductive success (Schulte and Simons 2016).

Role of heterogeneous landscapes for urban breeding shorebirds

Beach-nesting birds are in sharp decline worldwide, largely due to habitat degradation and loss from urbanization (Gibson et al. 2018). Although human disturbance usually reduces breeding performance by limiting foraging behavior, prey availability, nest attendance and chick brooding (Boyle and Samson 1985; Defeo et al. 2009; Martín et al. 2015; Schlacher et al. 2016), we have demonstrated here that shorebirds may be able to use alternative, less-disturbed and protected environments around the nesting site in order to breed in urban beaches. This finding may suggest that when suitable nesting and foraging habitats are available within a relative short distance, limited levels of disturbance could be counterbalanced. In this study, sandy beaches, rocky shores and a marine protected island nearby were considered important habitat patches for oystercatchers. By extrapolation, other habitats elsewhere such as mudflats, coastal grasslands, and salt marshes may play similar roles during the breeding period of shorebirds and deserve efforts for conservation. However, species may vary in their tolerance to disturbance, and landscape features may be more influential over birds that feed their brood and are able to bring food from distant areas such as oystercatchers. Other shorebird species generally have precocial self-feeding chicks, which are incapable of moving long distances to feed and thus require immediate access to foraging areas.

Overall, the findings reported here broadly demonstrate that landscape heterogeneity is an important factor determining the success and persistence of breeding birds in urbanized areas. Importantly, considering that species restricted in habitat requirements or that nest on the ground are often the most severely affected by urbanization (Marzluff 2001; Bonier et al. 2007), we demonstrated that even a highly specialist bird breeding and foraging in the marine-terrestrial interface may benefit from landscape heterogeneity. Thus, as untouched wilderness areas become progressively rarer and coastal habitats are largely affected by the increasing urban population, maintenance of preserved habitat patches and landscape connectivity are essentials for the conservation of shorebirds.

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Availability of data and material Not applicable.

Code availability Not applicable.

Authors' contributions PHO conceived the study idea; BAL, GTN and PHO designed the study; BAL performed the monitoring of breeding activities and food remain collections; BAL, FMR, GTN and PHO performed the fieldwork to capture and mark birds; BAL, FMR and PHO performed the on-board expeditions to Ilha dos Lobos; FAF and LB provided logistical, financial and technical support for the stable isotope analysis, including data analysis; BAL analyzed the data and wrote the first draft of the manuscript. All authors reviewed and contributed to the successive versions.

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Declarations

Ethics approval The study was performed under the permits from *Instituto Chico Mendes de Conservação da Biodiversidade* (SISBIO 64234–1) and from the Animal Ethics Committee of the *Universidade Federal do Rio Grande do Sul*.

Consent to participate All the authors consent to participate of this study.

Consent for publication All the authors consent to publish this study.

Conflict of interest The authors declare that they have no conflict of interest.

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