

# Breeding habitats, phenology and size of a resident population of Two-banded Plover (*Charadrius falklandicus*) at the northern edge of its distribution

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**Abstract** The central-peripheral hypothesis states that the demographic performance of a species decreases from the centre to the edge of its range. Peripheral populations are often smaller and tend to occur under different and suboptimal conditions from those of core populations. Peripheral populations can also coexist during part of their annual cycle with populations from the core of the species' range. Studies on peripheral populations are thus valuable for broadly understanding ecological and evolutionary processes. The Two-banded Plover (TWBP, *Charadrius falklandicus*, Charadriidae) is an endemic South American shorebird that breeds in Argentine and Chilean Patagonia and migrates northward during the Austral winter. There are breeding records, however, from Lagoa do Peixe National Park in southern Brazil. In this study, we (i) mapped TWBP nests, (ii) characterised their reproductive biology and nesting habitats, (iii) colour-marked birds and evaluated their seasonal occurrence patterns and (iv) estimated the size of the Brazilian population by combining supervised habitat classification analyses and generalised additive models. We estimated that the Brazilian population has 55 (95% CI: 44.1–66.6) breeding pairs and found that the length of their breeding season was roughly 5 months, spanning the Austral spring and summer. The population's nesting habitat differed, and their apparent reproductive success was lower than that of core populations. Unlike more southerly populations, the results of our mark-resighting efforts demonstrate that the Brazilian population is sedentary. Taken together, these results indicate that the Brazilian TWBP population seems geographically isolated from the species' southernmost core populations, resulting in a heteropatric distribution. Furthermore, differences in nesting habitat and year-round residency indicate that this peripheral population is ecologically distinct. The marked behavioural and ecological differences combined with the small population at the northern edge of the TWBP distribution support the central-peripheral hypothesis in a Neotropical system. Abstract in Portuguese is available with online material

**Key words:** abundance, central-peripheral hypothesis, heteropatric distribution, peripheral population, population estimates, shorebirds.

## INTRODUCTION

The central-peripheral hypothesis states that the demographic performance of a species decreases from the centre to the edge of its range (Sagarin & Gaines 2002; Pironon *et al.* 2017). Peripheral populations are often assumed to occur under different and less optimal conditions than those of a species' core populations (e.g. Safriel *et al.* 1994; Lesica & Allendorf 1995). Thus, they are often relatively smaller (Mayr 1965) and can differ genetically and

ecologically due to the effects of isolation, genetic drift and distinct natural selection regimes (Schwartz *et al.* 2003; Eckert *et al.* 2008). Peripheral populations are also likely to evolve more resistance to extreme conditions, with traits that may be crucial for the species as a whole to adapt to environmental change (Macdonald *et al.* 2017). As a result, peripheral populations are worthy of protection, especially when the global population is stable in the centre of its range (Lesica & Allendorf 1995).

The ranges of peripheral populations may adjoin those of a species' core population or coexist with individuals from the core population during part of

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their annual cycle, with some peripheral populations reproducing during different periods (allochryony) or at different sites (parapatry or heteropatry; Winker 2000; Jahn *et al.* 2010). In a heteropatric distribution, peripheral and core populations may be sympatric/syntopic during the non-breeding period but allopatric during the breeding season (Winker 2010). In this scenario, even in sympatry, organisms from distinct populations can co-occur during distinct phases of their annual cycles. This phenomenon has been documented in bird species from different lineages in which at least one of a species' populations is migratory (i.e. partial migration; Faria *et al.* 2010; Reppening & Fontana 2013). In this case, for instance, resident and migratory birds may coexist when residents are establishing breeding territories and migratory populations are refuelling for migration. These differences can result in behavioural barriers to dispersal and gene flow between core and peripheral populations (Botero-Delgado *et al.* 2020).

Since peripheral populations tend to be small and isolated, their occurrence patterns, size and demographic parameters are frequently unknown. These parameters, however, are key to the development of conservation strategies and management actions (e.g. Barbosa *et al.* 2010). In addition, the long-term conservation of species is likely to depend on the protection of distinct populations (Lesica & Allendorf 1995). Therefore, information on breeding biology and population size can be used to manage small and peripheral populations that can be vulnerable to localised threats or stochastic events (Andres *et al.* 2012).

Shorebirds are among the most threatened birds on the planet (Piersma 2006). Around half of all known shorebird populations are declining or lack enough information to accurately characterise their population dynamics (Colwell 2010; Simmons *et al.* 2015). The main causes of these declines are habitat loss and fragmentation, especially due to climate change and human development (Kirby *et al.* 2008; Colwell 2010). Less is known about South American shorebirds than shorebirds from any other continent (Piersma *et al.* 1997), and little new information has been gathered over the last few decades (Colwell & Haig 2019). This is mainly due to the lack of long-term monitoring programmes and funding for studies of South American species (Stroud *et al.* 2006).

The Two-banded Plover (TWBP) *Charadrius falklandicus* (Charadriidae) is a species with particularly little information available about its biology. TWBP are small Neotropical shorebirds endemic to southern South America (Hayman *et al.* 1986; Wiersma *et al.* 2020). They breed in the highest concentrations in Argentine and Chilean Patagonia, but some populations also breed on the Falkland/Malvinas Islands (St. Clair 2010). The breeding season of both the insular and continental TWBP populations occurs

from September to January (St. Clair 2010; Hevia 2013) and chicks are precocial and nidifugous (Colwell & Haig 2019). While the species has not been classified as globally threatened (Woods & Woods 1997), there is little recent information available about TWBP population trends, size or potential threats.

Studies on seasonal records and counts indicate that at least some of the Patagonian TWBP populations migrate northward after the breeding season, reaching as far north as the coasts of Uruguay and southern Brazil on the Atlantic coast (Vooren & Chiaradia 1990; Alfaro *et al.* 2008) and northern Chile on the Pacific coast (Hevia 2018). The Falkland/Malvinas Islands population may be sedentary (Woods & Woods 1997; St. Clair 2010), however, as has also been suggested for some continental populations from central Argentina (Nores & Yzurieta 1975; Torres & Michelutti 2006).

Within the past few decades, nesting records at the northern edge of the TWBP wintering distribution have been reported (Resende & Leeuwenberg 1989; Alfaro *et al.* 2008; Scherer *et al.* 2013). Alfaro *et al.* (2008) mentioned a single breeding record in Uruguay, which was regarded as a 'very unusual event'. In Brazil, a male with active gonads was collected in December 1974 by Belton (1994), and the first breeding record was confirmed in 1984 (Resende & Leeuwenberg 1989). Almost twenty years later, Scherer *et al.* (2013) found a single nest in 2011 at Lagoa do Peixe National Park (NP), a protected area in the Rio Grande do Sul state in southern Brazil. These studies have reported little information about the breeding biology of these northern breeders, and we thus lack knowledge about how consistently the species breeds in the region or the ecology of this putative breeding population. This important knowledge gap precludes inferences about the biological importance and distinctiveness of the TWBP breeding in southern Brazil and hinders potential conservation efforts or strategies.

In this context, we monitored TWBP breeding at Lagoa do Peixe NP during the 2019–20 breeding season. We describe the breeding phenology, productivity and seasonal occurrence patterns of this peripheral population, as well as model their presence as a function of habitat in order to provide estimates on the number of TWBP breeding pairs in southern Brazil. Following the central-peripheral hypothesis, we expected (i) lower fitness (i.e. breeding success), (ii) smaller population size and (iii) differences in habitat and nest-site characteristics in comparison with TWBP core populations. Taken together, our study will provide important insights into the ecology of species at the periphery of their ranges and a baseline for the conservation of this small but potentially important population of a Neotropical shorebird.

## METHODS

### Study area

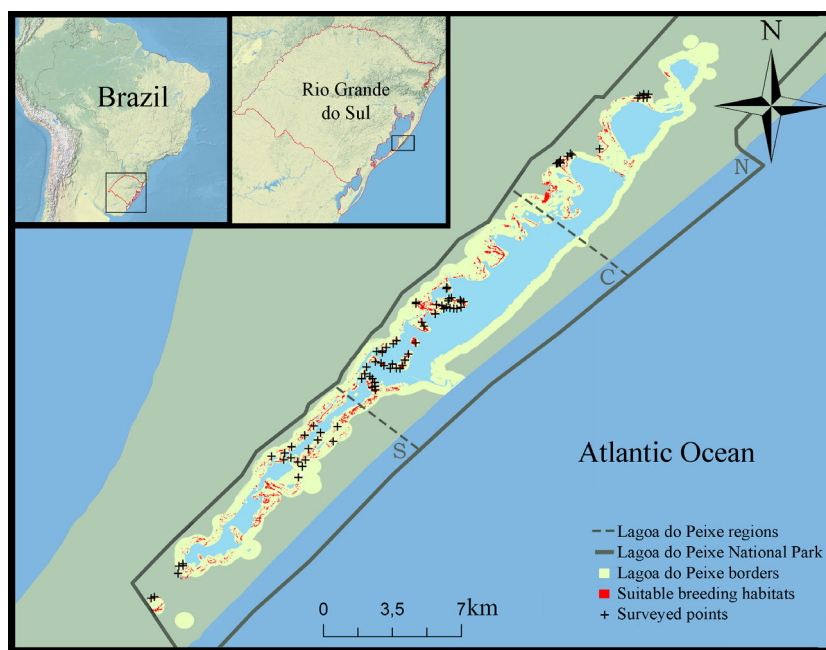
We conducted our study at Lagoa do Peixe NP, which is located on the central coast of the Rio Grande do Sul (RS) state in southern Brazil (31°15'S; 50°55'W, Fig. 1). Lagoa do Peixe NP extends across 36 722 ha and is mainly composed of coastal environments, such as marine sandy beaches, lagoons, dunes, wetlands, saltmarshes, *restinga* forest patches and coastal grasslands. The lagoon (Lagoa do Peixe) is ~35 km in length with an ephemeral connection to the ocean through a small inlet (Arejano 2006). The lagoon's hydrodynamics are influenced mainly by weather regimes, *that is* rainfall and winds, and it can provide mudflats where thousands of waterbirds feed. The lagoon's margins are composed of saltmarshes and grasslands, which are often flooded during the months of greatest precipitation and wind (e.g. during the passage of cold fronts from June to October; Klein 1998).

The saltmarshes are discontinuously distributed across the region resulting from variation in topography and the duration of saltwater submersion (Costa *et al.* 2003). The main saltmarshes are dominated by *Spartina densiflora* and *Salicornia neei*; *S. neei* is dominant in sites with longer periods of inundation and higher salinities (Costa 1997; Costa *et al.* 2019). Small islands have formed in the central and southern portions of the lagoon, comprised mostly of saltmarshes along their borders (Costa & Tagliani 2011) and low grasslands in their interiors (~5 cm height, F.A. Faria,

pers. obs. 2019). A salinity gradient exists dividing the lagoon into three main regions: the northern portion is limnetic due to its irregular borders and freshwater inflow, while the central portion is euryhaline, and the southern portion mesohaline (Trucollo 1993; Costa & Tagliani 2011). Lagoa do Peixe NP is a Ramsar Site and since 1990 has been part of the Western Hemispheric Shorebird Reserve Network due to its hemispheric importance for migratory shorebird populations (Nascimento 1995; WHSRN 2020).

### Nest site and territory characterisation

From October 2019 to February 2020, we systematically searched for TWBP nests and territories. We searched for territories based on landscape characteristics and guided by the knowledge of sites with couples and small chick (newly hatched) found in the previous reproductive season (2018–2019). As many as four researchers searched on foot for nests. We classified TWBP at each potential breeding site as present/absent based on our observations of territorial behaviours, *sensu* Colwell and Haig (2019). If territorial TWBP were observed at a given site, we backtracked ~150 m and used binoculars to observe potential breeding behaviours (i.e. incubating, courtship, territory defence). It is very unlikely that a site was misclassified as absent, due to (i) the active and vocal behaviour of plovers when researchers were present, and (ii) the frequent presence of the authors during the breeding season. Once a nest was



**Fig. 1.** Map of the study area in Lagoa do Peixe National Park (solid lines). Dashed lines represent Lagoa do Peixe National Park regions (North—N; Central—C and South—S). Surveyed potential breeding habitats of Two-banded Plover (*Charadrius falklandicus*) are represented by the + symbol. The light green line represents the 300-m waterbody buffer used in habitat classification. The red areas represent unsurveyed, but suitable TWBP breeding habitats modelled using satellite images and supervised classification models. Inset map: location of the study area within South America (upper left) and Rio Grande do Sul state, Brazil.

detected, we recorded (i) the number of eggs, (ii) the habitat type and (iii) its coordinates.

### Breeding biology and nest survival

In order to monitor breeding pairs, we captured 22 adults and marked them with a unique combination of coloured leg bands. We captured the birds at night with dip nets and a spotlight, and during the day with 5 × 12 m whoosh nets with 40 mm mesh. In addition, we mapped the size of six territories defended by breeding pairs. For each of these six territories, we delineated the maximum extent of the area where plovers exhibited defensive behaviours and plotted the coordinates to generate a polygon in ArcMap 10.8 with which to estimate the size of territory.

To estimate breeding phenology, we used active nests from the incubation through chick phases (non-flying), as well as photographic records of young before their first pre-juvenile moult (FPJ, *sensu* Wolfé *et al.* 2010). We used primary data collected from 2019 to 2020 ( $n = 17$ ) complemented with photo records from Lagoa do Peixe NP in the WikiAves ([www.wikiaves.com.br](http://www.wikiaves.com.br)) database (2010–2020,  $n = 5$ ). For three nests, we estimated the lay date by floating the eggs following Hevia (2013) and adapted from Noszály and Székely (1993) and Székely and Kosztolányi (2006).

To monitor and estimate nest success, we visited active nests, on average, every 6 days (range: 1–22 days). We estimated nest success rates using a known-fate model in Program MARK (White & Burnham 1999). We used the resulting daily survival rate (DSR) to estimate cumulative probabilities of nest survival. We determined a nest's fate using two potential lines of evidence: (i) the observation of at least one chick in the nest or in the vicinity of the nest; (ii) the observation of the breeding pair displaying, performing distraction flights or mobbing. Nests were considered to have failed if they flooded, disappeared before the expected hatch date, were deserted or trampled by cattle, or when a new nest was found nearby occupied by the same breeding pair. We considered the incubation phase to be the period between when the final egg was laid and the hatch of the first egg ( $\mu = 29$  days; St. Clair 2010). Finally, in order to direct comparison with previous studies, we also calculated the apparent success as the number of successful nests divided by the total number of nests (i.e. traditional method).

### Occurrence patterns

We combined year-round resightings of colour-marked TWBP with occurrence records in the Rio Grande do Sul state from eBird and WikiAves (2010–2020). Our resighting efforts consisted of 25 surveys spanning 2–8 days in field. We only considered photographic records from eBird and WikiAves with location and date information ( $n = 266$ ). Multiple registrations from the same location on the same day were discarded. We considered in the analysis (i) the entire Rio Grande do Sul state; (ii) the municipalities of Tavares and Mostardas, which comprise Lagoa do Peixe

NP; and (iii) the Rio Grande do Sul state outside of Tavares and Mostardas.

### GIS analysis

To assess the habitats used by TWBP during the breeding season, we obtained freely available Sentinel-2 satellite images (<http://glovis.usgs.gov>). The Sentinel-2 satellite provides high-resolution ( $\sim 10$  m<sup>2</sup>) multispectral imagery with 13 bands in the visible, near infrared, and shortwave infrared parts of the light spectrum (Immordino *et al.* 2019). Cloud-free images were obtained from the middle of our field survey period (11 December 2019). Prior to performing our habitat classification, we limited our analysis to the borders of Lagoa do Peixe NP. Subsetting increases overall classification accuracy, reducing the numbers of land-cover types and spectral variation (Bhattarai & Giri 2011). We generated multispectral images with bands 8, 4 and 3, as near infrared is efficient at detecting different vegetation types as well exposed soil (e.g. Stratoulas *et al.* 2015). These bands were used previously for saltmarsh habitat classification in southern Brazil (Nogueira & Costa 2003).

We used supervised classification models based on a maximum-likelihood algorithm to classify habitat types. This process involves translating the pixel values of a satellite image into distinct habitat categories (Horning *et al.* 2010) and allows the use of known breeding territories as 'training sites', as we confirmed land-cover type of each territory during our surveys. We performed a first classification to detect waterbodies inside the study site. Then, we applied a 300-m buffer around these waterbodies—based on the maximum distance of a nest from a waterbody—and classified the remaining habitats to determine their extent.

For each patch of breeding habitat, we used the central coordinates to calculate the (i) location (i.e. mainland *vs.* island); (ii) region (i.e. south, central or north Lagoa do Peixe NP); (iii) size (in ha); (iv) distance from the nearest waterbody; and (v) distance from the inlet to the ocean. For habitat size, we used pixel count of each habitat type multiplied by the image's spatial resolution. All GIS analyses were performed in ArcMap 10.8.

### Habitat modelling

We used generalised additive models (GAMs) to model the probability of occurrence of TWBP pairs in Lagoa do Peixe NP in relation to variables obtained from our GIS analyses. We tested the additive effects of five variables on the presence/absence of TWBP at 66 potential sites. We also included the distance to nearest occupied site to account for the potential semi-coloniality of TWBP (Patrick & Colwell 2017). We used GAMs with a binomial error structure (Brotons *et al.* 2004). Model fitting was carried out in the R software (v. 4.0; R Core Team 2020) using the 'mgcv' package (Wood 2018). A stepwise procedure was used for model selection. We evaluated the performance of candidate models using minimised generalised cross-validation (GCV) scores and residual deviations (Wood 2017).



## Population estimates

After characterising TWBP breeding habitat, we used our classification model to estimate the extent of potential TWBP breeding sites in each of the three regions within Lagoa do Peixe. Then, in each potential TWBP breeding site that was not surveyed, we also considered the five spatial parameters mentioned. We considered patches of suitable habitat  $\geq 0.44$  ha (the minimum size of a measured territory) to be potential breeding sites. Then, we used our GAM model results to predict the occupancy of breeding pairs in each of the non-surveyed sites ( $n = 116$ ). Finally, we estimated the number of TWBP breeding pairs as the sum of our on-the-ground survey results and model predicted values. To obtain 95% confidence intervals, we used the error method defined by Brown *et al.* (2007), multiplying lower and upper limits by the sum of predicted values of suitable habitat patches  $\geq 0.44$  ha.

## RESULTS

### Nest site and territory characterisation

TWBP nests consisted of small depressions on bare ground in a characteristic transitional habitat—composed mainly of sparse *S. neei* and exposed salty, sandy soil or short grasses—adjacent to the coastal grasslands bordering the lagoon (Fig. 2a,b). The nests were an elementary lined or unlined structure (i.e. the *simple* type; *sensu* Simon & Pacheco 2005). Breeding pairs were also observed feeding on the patches of grasslands within their territories. During our surveys, we mapped a total of 66 areas

considered to be suitable breeding sites, with 18 characterised as effectively used by breeding TWBP. We recorded 13 occupied on the Central islands within Lagoa do Peixe and four in the Central mainland. Eleven nests were detected in the Central region, with one additional nest found in the South bordering the lagoon. No nests were detected in the North. Nests were 46–283 m from the lagoon (mean  $\pm$  SD =  $135.4 \pm 72.7$  m) and 5–134 m from the nearest waterbody ( $72.6 \pm 38.9$  m; Table 1). Breeding territories ranged from 0.44 to 1.81 ha ( $0.82 \pm 0.49$  ha,  $n = 6$ ).

### Breeding biology and nest survival

The length of the breeding season was estimated at 156 days (5.2 months), starting on 04 September and continuing through the Austral spring and summer until 07 February, when the last nesting activity was recorded. The period with the most intense nesting activity was from early October to November (Fig. 3). The earliest fledging record (i.e. a chick  $> 7$  days of age) occurred on 04 October. Two nests found in November and December were re-nesting attempts. Juveniles were recorded from the second week of January through March. The average clutch size was 2.3 eggs (range = 1–3).

The daily nest-survival rate (DSR) was 0.92 (95% CI: 0.83–0.96;  $n = 12$ ). The cumulative probability of nest survival (i.e. nest success) estimated across the breeding season was 0.104. Overall, apparent reproductive success was also low, since only 23.1% of nests found generated at least one chick.

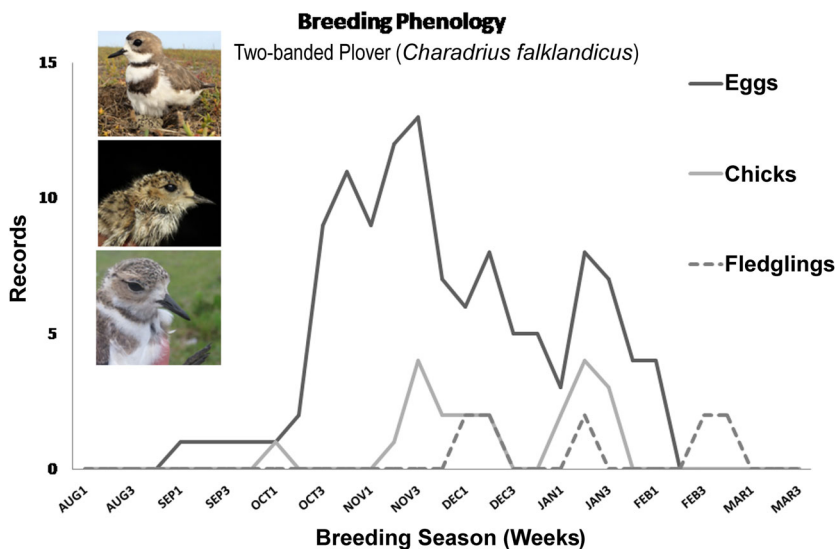
**Fig. 2.** A pair of Two-Banded Plover (*Charadrius falklandicus*) in their Brazilian breeding habitat composed of bare soil in a *Salicornia neei* patch. The transition to coastal grasslands (dotted line) and the lagoon in the background is shown (A). A typical TWBP nest characterised by a small depression in the soil with dry branches in a transition zone between *S. neei* and grasslands (B).



**Table 1.** Characterisation of Two-banded Plover (*Charadrius falklandicus*) nests in Lagoa do Peixe National Park, Rio Grande do Sul, Brazil

Nest	Number of eggs	Date first found	Region	Habitat	Habitat size (ha)	Distance to lagoon inlet (m)	Distance to lagoon (m)	Distance to nearest waterbody (m)
1	3	17 Oct 2019	Central	I	2.54	3973	60	5
2	3	17 Oct 2019	Central	I	2.54	3931	109	109
3	3	07 Nov 2019	Central	M	0.75	4434	134	78
4	1	08 Nov 2019	Central	I	2.03	3972	65	65
5	2	27 Nov 2019	Central	M	0.75	4457	158	59
6	3	27 Nov 2019	Central	I	2.54	391	126	84
7	2	08 Jan 2020	Southern	M	0.01	6502	283	19
8	2	09 Jan 2020	Central	M	0.75	4398	101	101
9	3	09 Jan 2020	Central	I	2.54	3878	184	99
10	2	16 Jan 2020	Central	M	0.49	234	46	46
11	2	16 Jan 2020	Central	I	5.99	2304	223	134

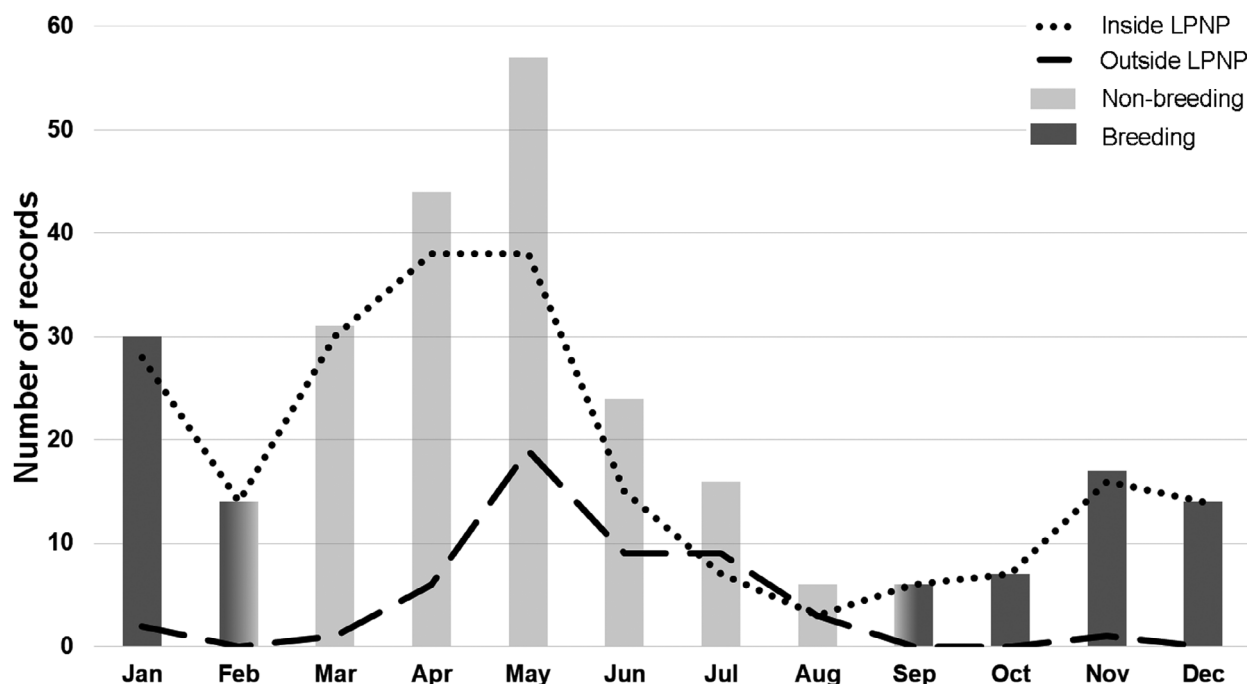
Habitat: I, Island; M, Mainland.

**Fig. 3.** Temporal distribution of active nests and fledglings of the Two-banded Plover (*Charadrius falklandicus*) in Lagoa do Peixe National Park throughout the breeding season from 2018 to 2020, complemented with photographic documentation of breeding activity from 2010 to 2020.

### Occurrence patterns

We identified 266 records of TWBP in the Rio Grande do Sul state deposited in online platforms from 2010 to 2020. TWBP were detected year-round, with a peak in records from April to May. A total of 216 records (81.4%) were within Lagoa

do Peixe NP. In addition, 28.9% were recorded during the breeding season. Considering only TWBP records made outside the Lagoa do Peixe NP ( $n = 50$ ), 94% were during the non-breeding season. However, 96% of all records in the breeding season ( $n = 75$ ) were within Lagoa do Peixe NP (Fig. 4). Finally, we were able to resight 8



**Fig. 4.** Year-round occurrence patterns of the Two-banded Plover (*Charadrius falklandicus*) using data from the online repositories eBird and WikiAves from 2010 to 2020. Vertical bars indicate total records for the entire Rio Grande do Sul state, Brazil. Dark grey represents the breeding season, and light grey represents the non-breeding season. The dotted line indicates records just from Lagoa do Peixe National Park (NP), and the dashed line indicates records in Rio Grande do Sul outside of Lagoa do Peixe NP.

birds (36%) that we colour-marked during the non-breeding season, all still within the borders of Lagoa do Peixe NP.

### GIS analysis

To assess the quality of our training sites, we compared the results of our classification model with the information obtained *in situ*. We found that 88.3% ( $n = 66$ , of which 10, 39 and 17 belonged to the North, Central and South regions, respectively) of the potential breeding sites surveyed were correctly classified as suitable. The supervised model classified 329.8 ha of habitat as suitable for TWBP breeding within Lagoa do Peixe NP. The Central region held 42% of all suitable areas, followed by the South with 37%. Habitat sizes ranged from 0.01 to 10.25 ha ( $0.16 \pm 0.57$  ha). Only 0.7% of habitats were  $> 1$  ha.

### Habitat modelling

The top model included the variables ‘region,’ ‘habitat size,’ ‘distance to nearest waterbody’ and ‘distance to the lagoon inlet,’ although only the latter was a significant predictor. Also, the ‘distance to nearest occupied site’ did not improve the model, so

we used the most parsimonious one for predictions (Table 2).

### Population estimates

We estimated the density of breeding pairs as  $0.186$  birds  $\text{ha}^{-1}$  in the Central region and

**Table 2.** Generalised additive model results for Two-banded Plover (*Charadrius falklandicus*) nest-site selection using a binomial error structure. area\_h: size of each suitable habitat patch in hectares; dist\_wat: distance to nearest waterbody in metres; dist\_inlet: distance to Lagoa do Peixe inlet in metres

	Parameter estimate	Standard error	<i>P</i>
(Intercept)	$-1.13 \times 10^2$	2.63	1.00
region_Central	$1.09 \times 10^2$	$2.12 \times 10^7$	1.00
region_South	$1.01 \times 10^2$	3.44	1.00
area_h	0.22	0.22	0.30
dist_inlet	$1.4 \times 10^{-3}$	$5.64 \times 10^{-4}$	0.01*
<b>Approximate signif. of smooth terms:</b>	<b>edf</b>	<b>Chi.sq</b>	<b><i>P</i></b>
s(dist_wat)	3.79	4.80	0.41
$R^2$ (adj) = 0.424	Deviance explained = 47.2%		

Signif. codes: \* $P < 0.05$ .

**Table 3.** Estimates of the number of Two-banded Plover (TWBP, *Charadrius falklandicus*) breeding pairs at Lagoa do Peixe National Park (NP), Rio Grande do Sul, Brazil

Region	Southern	Central	Northern	Total
Counted	1	17	0	18
Estimated	12.5	22.5	2 (0–4.7)	37
(IC95%)	(7.4– 17.6)	(18.7– 26.3)		(26.1– 48.6)
Total	13.5	39.5	2 (0–4.7)	55
	(8.4– 18.6)	(35.7– 43.3)		(44.1– 66.6)

Estimates were generated with supervised classification model confined to the three regions of Lagoa do Peixe NP.

0.01 birds ha<sup>-1</sup> in the South. The number of breeding pairs estimated across non-surveyed sites was 37 (95% CI: 26.1–48.6). Therefore, the total estimate of the resident TWBP population inhabiting Lagoa do Peixe NP was 55 (95% CI: 44.1–66.6) breeding pairs (Table 3).

## DISCUSSION

We provide information about a heteropatric population of non-migratory Two-banded Plovers and its breeding habitat at the species' northern range limit. We found that this population is smaller than, and uses a unique habitat from, known populations in the core and southern portions of the species' breeding range. The population's apparent nest success was also lower than that of the Patagonian core population. This information enhances our knowledge of the biology of Neotropical shorebirds and provides support for the central-peripheral hypothesis (Sagarin & Gaines 2002).

TWBP nests in Brazil—which were small scrapes in bare ground—were different from previous descriptions of nests from more southerly latitudes. Nests of the core population are conspicuous platforms built with sticks, seaweed and shells (García-Peña *et al.* 2008; Hevia 2013). The breeding habitats of the two populations also differed: in Brazil, TWBP breeding habitat was comprised by vegetated saltmarshes adjacent to grasslands, while in Patagonia, nests are built mainly on gravel and boulder beaches along shorelines (García-Peña *et al.* 2008; Hevia 2013). Information on territory size of most plovers are usually not reported (Stenzel & Page 2019) and we were unable to find previous information on TWBP territory sizes with which to compare our data.

We documented an apparent nest success of 23% in Brazil, which was lower than has been reported in Patagonian core populations, where breeding success

ranged between 37% and 67% across three years (García-Peña *et al.* 2008). However, our findings were similar to estimates of TWBP reproductive success from the Falkland/Malvinas Islands population (27%,  $n = 294$ ; St. Clair 2010). The nest success of Brazilian TWBP, based on our extrapolated survival estimates (10.1%), was also similar to previous studies from other small or declining plover populations (e.g. Norte & Ramos 2004, for Kentish Plover; Zefania *et al.* 2008, for Madagascar Plover).

Overall, only 0.89% of the Lagoa de Peixe was classified as suitable habitat for TWBP. This was likely caused by a combination of factors, including topography, precipitation and the wind regimes that influence the distribution of salinity and saltmarsh habitats around the lagoon (Trucollo 1993; Costa & Tagliani 2011). The relatively exposed habitats provided by *S. neei* patches are restricted to sites with extended periods of saltwater flooding, which constrains *S. densiflora* growth. Without prolonged flooding, *S. neei* facilitates the recruitment of *S. densiflora*, which dominates higher marshes and potentially competitively displaces *S. neei* (Alberti *et al.* 2008). TWBP were thus likely concentrated in the Central portion of the lagoon because of the higher salinity of the lagoon in this region.

We did not detect that TWBP selected insular *versus* mainland habitats, although our models indicated that the probability of occupancy was negatively related to distance to waterbodies. We also did not observe that TWBP selected nest sites based on distance to conspecific neighbours. Despite the fact that plover species may breed semi-colonially, this pattern seems strongly related to population size and is more evident in core populations with higher breeding densities (Patrick & Colwell 2017).

Although we did not directly document any predation events, predation is likely the primary cause of nest failure and potentially accounted for 60% of failed nests. Given the overall low nest-survival rates that we documented, identifying predator species and monitoring predation rates would help management decision making for the TWBP population in Brazil. In particular, investigating the influence that the relative size, shape and slope of nesting habitats have on TWBP nest-site selection and their ability to detect (and evade) predators can have crucial management implications and should be a priority (Whittingham *et al.* 2002; Muir & Colwell 2010). Both the number of nests and hatching success appeared to increase during the second half of the TWBP breeding season, but we did not assess this in our tests. The area around the lagoon is more prone to flooding early in the breeding season and, accordingly, the first nest we found, on 17 October, failed due to flooding. This is likely due to (i) higher winter precipitation that increases the height of the lagoon (Klein 1998);



(ii) the limited potential for evaporation during the winter and spring; and (iii) the intermittent inlet that connects the lagoon with the ocean remains closed during winter. In most of the years, the inlet connecting the lagoon to the ocean is artificially opened with the aid of a backhoe to allow waterflow and the entrance of shrimp larvae in late July (Arejano 2006). As a result, during the early TWBP breeding period in late September and early October, some potential nest sites are still flooded and only become available over the course of the season.

The length of the breeding season and its relative timing within the annual cycle of the Brazilian population was similar to TWBP populations monitored in Falkland/Malvinas Is. and along the Patagonian coast (García-Peña *et al.* 2008; St. Clair 2010; Hevia 2013). In this sense, the combination of breeding synchronicity and occurrence patterns suggests that the Brazilian population is a year-round resident and isolated from core TWBP populations. This means that the mixed migration strategies employed by the species result in a heteropatric distribution.

Although we have not analysed the evolutionary history of the Brazilian population, a number of different hypotheses could explain its distribution. It could either be a relictual population, with extinct populations previously having occurred throughout the entire species' distribution. Conversely, it could be the result of a more recent colonisation, with individuals from the core migratory population having ceased migrating and begun breeding in their wintering area. The loss of migratory behaviour can evolve rapidly (Pulido & Berthold 2010), and studies have shown shifts in migration strategies leading to the establishment of populations on the non-breeding grounds of numerous taxa, including flycatchers (Gómez-Bahamón *et al.* 2020), swallows (Winkler *et al.* 2017) and raptors (Bildstein 2004). However, this phenomenon still lacks documentation in shorebirds.

Despite the lack of population trend information, the long-term viability of this population is a cause of concern due to its small size and the limited extent of its habitat. For example, the lagoon within Lagoa de Peixe NP possesses unique characteristics—such as its ephemeral connection with the sea—not observed in any other lagoon along the southern Brazilian Coastal Plain (Arejano 2006). TWBP are thus unlikely to expand their range to other Brazilian lagoons. Even within Lagoa de Peixe NP, anthropogenic forces are a threat to tidal marshes, especially climate change (Greenberg 2006; Wiest *et al.* 2016). Because tidal marshes are especially sensitive to sea level rise (Schuerch *et al.* 2013), increases in flooding frequency and severity may affect the hydrodynamics of the lagoon, changing salinity patterns and, as a

result, the vegetation structure of the saltmarshes used by TWBP.

Taken together, our results suggest that TWBP breeding in Brazil conform to the central-peripheral hypothesis. Future efforts should therefore focus on developing a deeper understanding of the environmental factors influencing their population dynamics and the degree to which they are isolated from other TWBP populations in the core of the species' range. Irrespective of these findings, the distinct breeding habitat and behavioural differences of the Brazilian TWBP population suggest that they should be treated as a unique ecological management unit.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## AUTHOR CONTRIBUTIONS

**Fernando Faria:** Conceptualization (equal); Formal analysis (lead); Funding acquisition (supporting); Methodology (equal); Resources (supporting); Writing-original draft (lead). **Márcio Repenning:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Methodology (equal); Writing-review & editing (supporting). **Guilherme Tavares Nunes:** Conceptualization

(supporting); Methodology (supporting); Supervision (supporting); Writing-review & editing (supporting).  
**Nathan Senner:** Conceptualization (equal); Formal analysis (equal); Methodology (equal); Supervision (supporting); Writing-review & editing (equal).  
**Leandro Bugoni:** Conceptualization (equal); Methodology (supporting); Supervision (lead); Writing-review & editing (supporting).

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