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Cover illustration: Silvery Grebe (*Podiceps occipitalis*) by Tatiana Corbo Codazzi

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Editorial

# EL HORNERO IN TWO LANGUAGES

Lucia Mentesana

Editor-in-Chief, El Hornero. Scientific Department, Aves Argentinas
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When we think of a scientific journal, we usually think of the articles it publishes. However, a journal is much more than that. It is a community of people who generate knowledge, evaluate it, edit it, communicate it, and ultimately use it to inspire new questions. In this sense, each volume of *El Hornero* represents a collective effort, bringing together contributions from many different perspectives to build and disseminate knowledge about Neotropical birds.

In recent years, *El Hornero* has undergone a period of transformation and growth (Ursino & Roesler 2025). We have strengthened our editorial processes, expanded our visibility, and continued working to provide a journal that is rigorous, accessible, and relevant to the scientific community. Today, we are pleased to share a new step in this journey: beginning with this volume, all articles published in the journal will be available in both Spanish and English.

This decision reflects a clear goal: we want the knowledge generated by our community to reach a broader audience, transcend geographical and linguistic boundaries, and increase its international visibility and impact. English is currently the predominant language of scientific communication, and offering bilingual versions will facilitate the dissemination of research conducted in our region to a wider global audience.

At the same time, this change does not mean abandoning our roots. Since its inception, Spanish has been a fundamental part of the identity of *El Hornero*. Maintaining it as a language of publication is a way of preserving a tradition that spans more than a century and ensuring that scientific knowledge remains accessible to those who study, research, manage, and are interested in birds throughout Latin America.

We believe that science is strongest when it is inclusive and accessible. Publishing in two languages allows us to pursue both goals: maintaining our commitment to the Spanish-speaking community while opening new opportunities for the international dissemination of the work we receive and publish.

Achieving this new objective required reorganizing editorial workflows, building new collaborations, and, above all, relying on a dedicated team of English-speaking volunteers whose commitment makes each issue possible. To everyone who contributes to this effort, and to those who have recently joined *El Hornero*, we extend our sincere gratitude.

We hope that this new stage will help strengthen the role of *El Hornero* as a meeting place for Neotropical ornithology.

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# CAVITY-NESTING BIRDS: EVALUATING THE USE OF NATIVE AND EXOTIC TREE SPECIES IN THE ESPINAL ECOREGION

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**ABSTRACT:** This study assessed the use of trees for nesting by cavity-nesting birds in the Espinal ecoregion, Argentina. We analyzed data from 264 nests of tree cavity-users (114 woodpecker nests, and 150 from secondary cavity-nesting birds) found over a 49-year period (1970–2019) in a fragmented landscape. The main results showed that this group of birds makes greater nesting use of native trees, such as Chañar (*Geoffroea decorticans*) and Algarrobo (*Prosopis alba*), both live and standing dead, although the use of exotic trees was also recorded. Furthermore, secondary cavity-nesting birds showed a proportionally higher use of cavities generated by decomposition. These findings highlight the importance of retaining native, live, and standing dead trees in the landscape as key elements for the conservation of avifauna in fragmented landscapes.

**KEYWORDS:** *agroecosystems, Argentina, dry forests, nesting, reproductive biology*

Ecological studies on resource use for foraging, shelter, or nesting are one of the most effective ways to identify relationships among animal species within a given habitat (Atkinson et al. 2005, Ferger et al. 2014). Information on use of resources such as habitat types and anthropogenic disturbances can be effective for evaluating different responses of animal species to environmental change (Marzluff et al. 2004, Ossi et al. 2022). An example of this is tree cavities, which are an important resource in forests for many bird species that depend on them for nesting or shelter (Cockle et al. 2011, Schaaf et al. 2021). In this context, when cavity availability is limited, competition among species increases and reproductive opportunities are reduced, which can decrease the abundance of cavity-nesting birds (Brawn & Balda 1988, Newton 1994, Schaaf et al. 2021). This highlights that suitable cavities constitute a critical and potentially limiting resource, whose availability is key to understanding in modified landscapes (Newton 1994, Cockle et al. 2011).

Currently, approximately 18% of all bird species worldwide nest in tree cavities, with the greatest richness occurring in the Neotropics (van der Hoek et al. 2017). Within this group, primary cavity users can be distinguished, such as woodpeckers (Picidae), which excavate their own cavities for nesting or shelter; facultative excavators such as trogons (Trogonidae), which excavate or modify pre-existing cavities; and secondary users, within which there is a wide variety of taxa that use cavities generated by excavators or those created by decay and/or breakage of trees (Aitken & Martin 2008, Cornelius et al. 2008, van der Hoek et al. 2017, Di Sallo & Cockle 2025).

Because of these habitat requirements, this group of birds is often affected by the number of specific sites available for nesting. For example, bird species with greater body mass require cavities with larger entrances, which are usually found in trees of larger diameter, and this can significantly influence nest-site selection by secondary users (Renton et al. 2015, Bonaparte et al. 2020, Di Sallo & Cockle 2022). On

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the other hand, excavating birds also have specific requirements that influence nest-site selection, as they need large trees with a certain hardness to house cavities suitable for excavation (Jauregui et al. 2021, Di Sallo & Cockle 2025). However, large trees, which are crucial for housing such cavities and necessary for excavation, are the scarcest and most frequently removed due to various anthropogenic activities, such as agriculture, forestry, or replacement by commercial forest species (Manning & Lindenmayer 2009, Ibarra & Martin 2015, Schaaf et al. 2021).

For this group of birds, the loss of large native trees and standing dead trees in modified landscapes forces some bird species to depend on the use of exotic tree species for nesting (Zapponi et al. 2014, Bonaparte et al. 2020). The use of exotic trees for nesting has been recorded in several Neotropical species and may be associated with the expansion of anthropogenic activities where exotic vegetation is abundant, a pattern that is important to investigate in fragmented areas of Argentina (Jauregui et al. 2019, Maya-Elizarrarás et al. 2025). One of the Argentine forest ecoregions most affected by landscape transformation in recent decades is the Espinal (Nanni et al. 2020). Therefore, data on the relationships between avifauna and cavities in different tree species within this ecoregion have important conservation implications.

This study aims to describe the use of nesting sites by cavity-nesting birds in the Espinal ecoregion, seeking to determine the use of arboreal substrates in native and exotic species, as well as the condition of the tree (alive or standing dead). In addition, we examined whether secondary user birds (classified by body mass) differentially depend on cavities generated by decay or excavated by woodpeckers. Finally, we analyzed the importance of these relationships for avifaunal conservation in an ecosystem facing high levels of transformation in Argentina. This information may be fundamental for formulating better forest retention policies aimed at bird conservation.

## METHODS

### Study area

The work was carried out in the 'Médico Veterinario Martín R. de la Peña' Natural Reserve, a protected area of the Universidad Nacional del Litoral that covers an area of approximately 70 ha (31°20'S, 60°40'W). This reserve belongs to the Espinal Ecoregion and is located about 5 km from the city of Esperanza, in the center of Santa Fe province, Argentina (Fig. 1). The regional climate is subhumid, with mean annual temperatures of 20°C and rainfall that can exceed 1100 mm per year (Lovino et al. 2020). Regionally, the Espinal is

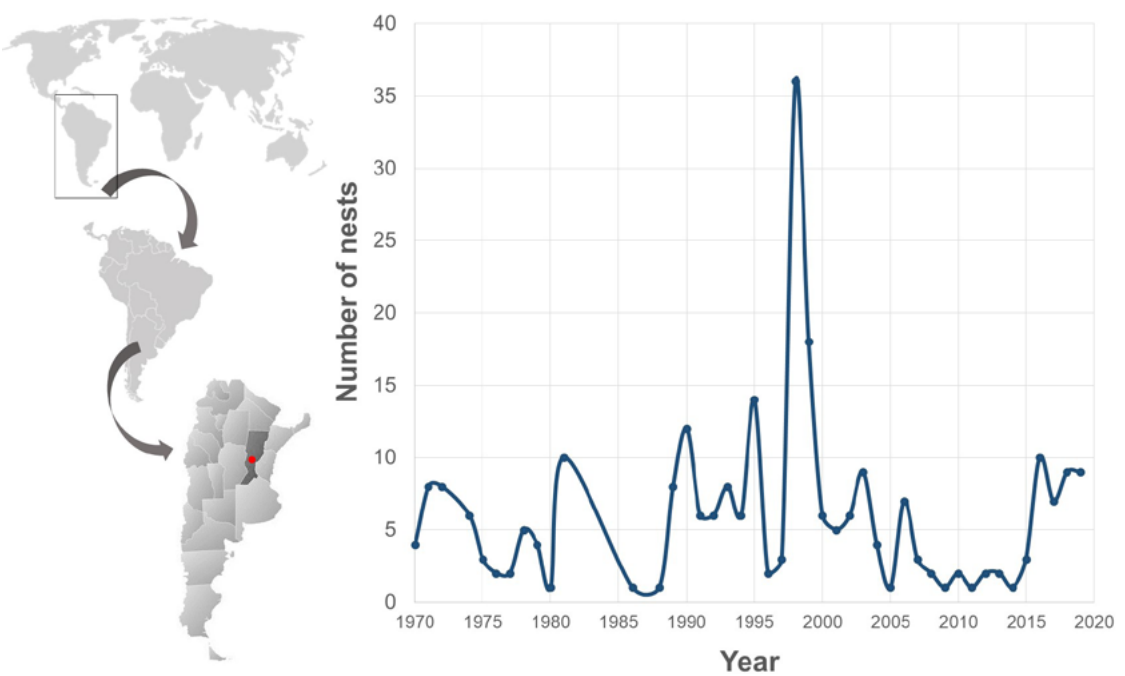


**Figure 1.** Study area and timeline of the total number of cavity-nesting bird nests found between 1970–2019 in the Espinal Ecoregion, Santa Fe province, Argentina.

a highly modified and fragmented landscape due to deforestation and intense agricultural and livestock exploitation, with little remaining intact forest. The vegetation of the reserve includes native species such as White Algarrobo (*Prosopis alba*), Chañar (*Geoffroea decorticans*), Tala (*Celtis tala*), Curupí (*Sapium haematospermum*), White Quebracho (*Aspidosperma quebracho-blanco*), and exotic species such as Eucalyptus (*Eucalyptus* sp.) and Chinaberry (*Melia azedarach*), constituting one of the forest remnants within this productive matrix (de la Peña & Pensiero 2003, Exner et al. 2004).

### Data collection and analysis

A dataset of cavity-nesting bird nests collected by one of the authors (MRDP) over a non-consecutive period of 49 years (between 1970 and 2019) was analyzed. Nesting data came from casual observations and surveys carried out in the study area during the breeding season (spring–summer), considering only cavities that presented minimum physical characteristics to allow nesting (an adequate entrance opening and a vertical depth greater than 5 cm). Cavities were recorded as active nests when reproductive evidence was observed (presence of eggs, nestlings, or adults carrying nesting material or food).

The main variables analyzed were bird species, type of cavity used (excavated or generated by decay), tree species type (native or exotic), and tree condition (alive or standing dead). For secondary users, we followed Cockle et al. (2015), separating them into three groups based on body mass: small birds (< 100 g), medium-sized birds (100–400 g), and large birds (> 400 g). This classification was adopted to increase the effective sample size within each category, allowing the grouping of data from species with a low number of individual nesting observations. Body mass for each bird species was obtained from Dunning (2007).

The data were analyzed using descriptive statistics, calculating the frequency of use of each category (cavity type, tree species, tree condition) for each bird group (woodpeckers and secondary users).

## RESULTS

During the study period, a total of 264 nests from tree cavities were recorded and characterized, and the number of findings fluctuated widely throughout the field sampling period (Fig. 1). Of this total, 114 nests of eight species of woodpeckers and 150 nests corresponding to 36 species of secondary cavity-using birds were identified. Among excavators, the species with the highest abundance of recorded nests were the Green-barred Woodpecker (*Colaptes melanochloros*, $n$ = 35) and the White-barred Piculet (*Picumnus cirratus*, $n$ = 25). With respect to secondary users, the abundance of nests found varied according to body size: among small-sized species, the most abundant were the White Monjita (*Xolmis irupero*, $n$ = 17) and the Saffron Finch (*Sicalis flaveola*, $n$ = 15); the Tropical Screech-Owl (*Megascops choliba*, $n$ = 10) was the species with the highest number of nest records in the medium-sized group; whereas the Black Vulture (*Coragyps atratus*, $n$ = 13) showed the highest abundance among species classified as large.

**Table 1.** Nests of cavity-nesting birds found between 1970–2019 in the Espinal Ecoregion, Santa Fe, Argentina. Common and scientific names are provided, along with the total number of nests found and the percentage of nests (relative to the total) in native and exotic trees, in excavated cavities (E) and decay-generated cavities (D), for each bird species.

| | Common name | Scientific name | Total nests | Native (%) | | Exotic (%) | |
|---|---|---|---|---|---|---|---|
| | | | | E | D | E | D |
| Primary cavity-using birds | Green-barred Woodpecker | *Colaptes melanochloros* | 35 | 86 | 0 | 14 | 0 |
| | White-barred Piculet | *Picumnus cirratus* | 25 | 96 | 0 | 4 | 0 |
| | White-fronted Woodpecker | *Melanerpes cactorum* | 24 | 71 | 0 | 29 | 0 |
| | Checkered woodpecker | *Veniliornis mixtus* | 10 | 80 | 0 | 20 | 0 |
| | White woodpecker | *Melanerpes candidus* | 4 | 50 | 0 | 50 | 0 |
| | Campo flicker | *Colaptes campestris* | 9 | 0 | 0 | 100 | 0 |
| | Cream-backed Woodpecker | *Campephilus leucopogon* | 5 | 100 | 0 | 0 | 0 |
| | Little woodpecker | *Veniliornis passerinus* | 2 | 100 | 0 | 0 | 0 |

| | | Common name | Scientific name | Total nests | Native (%) | | Exotic (%) | |
|---|---|---|---|---|---|---|---|---|
| | | | | | E | D | E | D |
| Secondary cavity-using birds | Small-sized | White Monjita | *Xolmis irupero* | 17 | 47 | 53 | 0 | 0 |
| | | Saffron finch | *Sicalis flaveola* | 15 | 67 | 33 | 0 | 0 |
| | | White-rumped swallow | *Tachycineta leucorrhoa* | 11 | 45 | 45 | 0 | 10 |
| | | Scimtar-billed woodcreeper | *Drymornis bridgesii* | 10 | 20 | 0 | 60 | 20 |
| | | Southern house wren | *Troglodytes musculus* | 10 | 60 | 40 | 0 | 0 |
| | | Narrow-billed woodcreeper | *Lepidocolaptes angustirostris* | 9 | 12 | 44 | 0 | 44 |
| | | Ferruginous Pygmy Owl | *Glaucidium brasilianum* | 3 | 0 | 34 | 33 | 33 |
| | | Chopi blackbird | *Gnorimopsar chopi* | 3 | 0 | 33 | 67 | 0 |
| | | Streaked flycatcher | *Myiodynastes maculatus* | 3 | 33 | 67 | 0 | 0 |
| | | Short-crested flycatcher | *Myiarchus ferox* | 2 | 0 | 100 | 0 | 0 |
| | | Swainson's flycatcher | *Myiarchus swainsoni* | 2 | 50 | 50 | 0 | 0 |
| | | House sparrow | *Passer domesticus* | 2 | 0 | 0 | 0 | 100 |
| | | Common starling | *Sturnus vulgaris* | 2 | 0 | 0 | 100 | 0 |
| | | Chaco earthcreeper | *Tarphonomus certhioides* | 2 | 0 | 100 | 0 | 0 |
| | | Great Rufous Woodcreeper | *Xiphocolaptes major* | 2 | 0 | 100 | 0 | 0 |
| | | Euler's Flycatcher | *Lathrotriccus euleri* | 1 | 0 | 100 | 0 | 0 |
| | | Tufted Tit-Spinetail | *Leptasthenura platensis* | 1 | 100 | 0 | 0 | 0 |
| | | Brown-crested Flycatcher | *Myiarchus tyrannulus* | 1 | 0 | 100 | 0 | 0 |
| | | Buff-browed Foliage-gleaner | *Syndactyla rufosuperciliata* | 1 | 0 | 100 | 0 | 0 |
| | | Black-crowned Tityra | *Tityra inquisitor* | 1 | 0 | 100 | 0 | 0 |
| | | Rufous-bellied Thrush | *Turdus rufiventris* | 1 | 0 | 0 | 0 | 100 |
| | | Grey Monjita | *Nengetus cinereus* | 1 | 0 | 0 | 0 | 100 |
| | Medium-sized | Tropical Screech Owl | *Megascops choliba* | 10 | 20 | 40 | 20 | 20 |
| | | Blue-crowned Parakeet | *Thectocercus acuticaudatus* | 4 | 0 | 50 | 25 | 25 |
| | | Ringed Teal | *Callonetta leucophrys* | 3 | 0 | 33 | 0 | 67 |
| | | American Kestrel | *Falco sparverius* | 3 | 0 | 33 | 0 | 67 |
| | | Eared Dove | *Zenaida auriculata* | 3 | 0 | 100 | 0 | 0 |
| | | Rock Dove | *Columba livia* | 1 | 0 | 100 | 0 | 0 |
| | | Chimango caracara | *Daptrius chimango* | 1 | 0 | 0 | 0 | 100 |
| | | White-eyed Parakeet | *Psittacara leucophthalmus* | 1 | 0 | 100 | 0 | 0 |
| Secondary cavity-using birds | Large-sized | Black vulture | *Coragyps atratus* | 13 | 0 | 23 | 0 | 77 |
| | | American Barn Owl | *Tyto furcata* | 5 | 0 | 20 | 0 | 80 |
| | | Turkey Vulture | *Cathartes aura* | 2 | 0 | 100 | 0 | 0 |
| | | Black-bellied Whistling Duck | *Dendrocygna autumnalis* | 2 | 0 | 0 | 0 | 100 |
| | | Muscovy Duck | *Cairina moschata* | 1 | 0 | 0 | 0 | 100 |
| | | Laughing Falcon | *Herpetotheres cachinnans* | 1 | 0 | 100 | 0 | 0 |

It should be noted that medium-sized species that are facultative users of tree cavities were also found, such as the Rufous-bellied Thrush (*Turdus rufiventris*) and the Rock Pigeon (*Columba livia*). Nests of the European Starling (*Sturnus vulgaris*), an exotic invasive species and a well-known user of tree cavities, were also found (Table 1 & Supplementary Material).

The analysis of secondary cavity-using birds ($n$ = 150 nests) showed a higher proportion of use of cavities generated by decay (66%), whereas the remaining nests used cavities excavated by woodpeckers (34%). In turn, the frequency of cavity use varied with body mass: small-sized birds, which constituted the most numerous group ($n$ = 100 nests), and medium-sized birds ($n$ = 26 nests) mostly used cavities generated by decay (54% and 81%, respectively); whereas large birds ($n$ = 24 nests) showed complete dependence on cavities generated by decay, with no nests recorded in cavities excavated by woodpeckers (Fig. 2, Table 1). Among secondary users that used cavities excavated by woodpeckers, most used those excavated by *Colaptes* sp. ($n$ = 48), whereas the Tufted Tit-Spinetail (*Leptasthenura platensis*) and the Northern House Wren (*Troglodytes aedon*) used cavities excavated by the White-fronted Woodpecker (*Melanerpes cactorum*; $n$ = 2); and only one cavity excavated by the White-barred Piculet (*Picumnus cirratus*) was used by the House Wren.

With respect to the tree species and condition used for nesting, both woodpeckers and secondary cavity-using birds showed a higher frequency of use of native trees (70%) compared with exotic trees (30%). In detail, woodpeckers recorded most of their nests in living trees (72%); whereas secondary cavity-using birds that used cavities generated by decay also nested mainly in living trees (61%), but showed a higher frequency of use of standing dead trees (39%) compared with woodpeckers (Fig. 2).

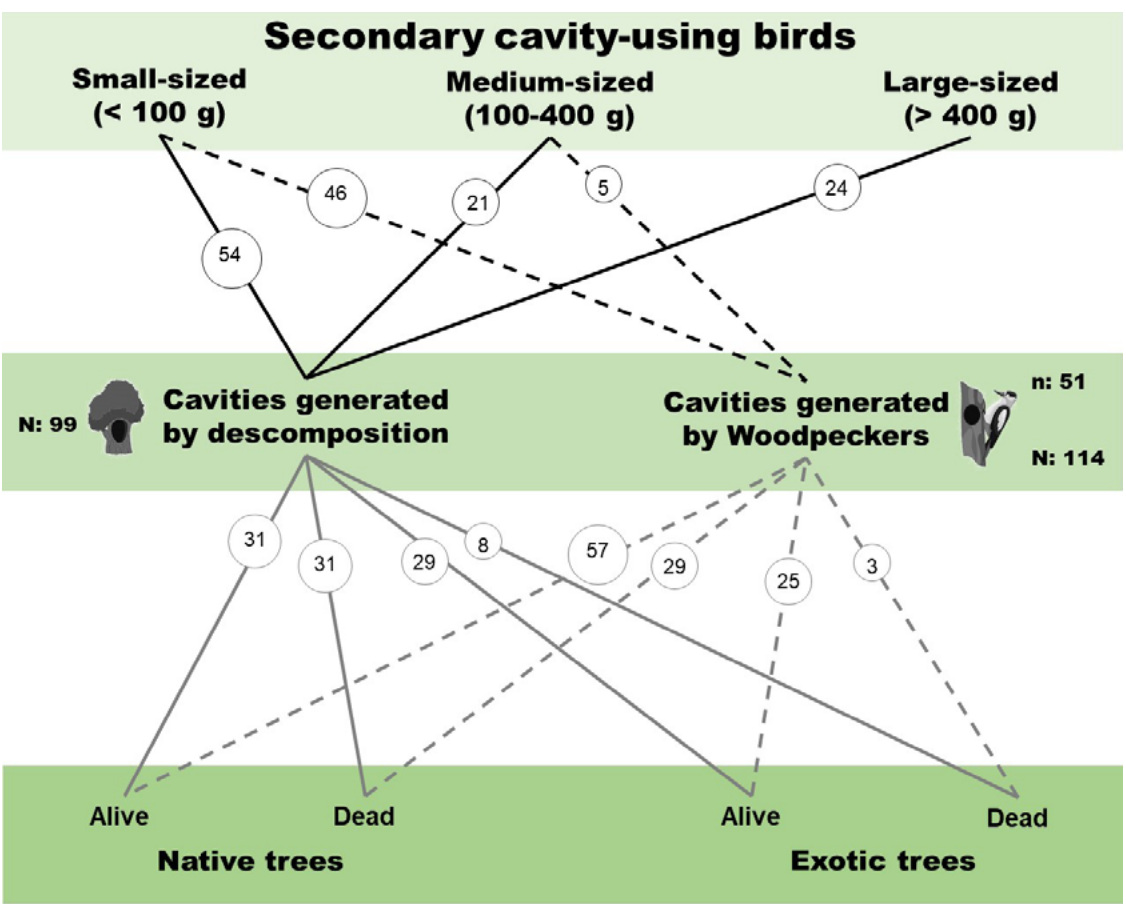


**Figure 2.** Schematic diagram of the total number of cavity-nesting bird nests found in the Espinal Ecoregion. The total number of nests (circles) is shown for woodpeckers (dashed lines) and secondary cavity-using birds (solid lines), separated by body mass. In addition, the total number of woodpecker nests found (N), the total number of these nests used by secondary cavity-using birds (n), and the type of arboreal substrate are detailed.

Native tree species, both living and standing dead, were mainly Chañar (*Geoffroea decorticans*, 37%), Algarrobo (*Prosopis alba*, 25%), and Curupí (*Sapium haematospermum*, 15%), whereas the remainder were White Quebracho (*Aspidosperma quebracho-blanco*), Red Quebracho (*Schinopsis balansae*), Ceibo (*Erythrina crista-galli*), and Willow (*Salix humboldtiana*). On the other hand, exotic living and standing dead trees used belonged mainly to Chinaberry (*Melia azedarach*, 60%), *Eucalyptus* sp. (22%), and Ash (*Fraxinus pennsylvanica*, 12%); whereas the remainder were species such as Mulberry (*Morus alba*) and Black Locust (*Gleditsia triacanthos*).

## DISCUSSION

This study evaluated the use of nesting resources by cavity-nesting birds in the Espinal ecoregion, an area characterized by a high rate of land-use conversion (Nanni et al. 2020). Specifically, Chañar (*Geoffroea decorticans*) and Algarrobo (*Prosopis alba*) stand out as the most frequently used native species. This pattern has also been reported in other ecoregions such as the Humid Chaco, where native trees of the genus *Prosopis* constitute a key nesting substrate, as their low wood density facilitates excavation by woodpeckers whilst providing cavities generated by decay that are suitable for non-excavating birds (Di Sallo & Cockle 2022, 2025).

Despite the higher proportion of use of native trees, the use of exotic trees for nesting suggests a degree of plasticity in certain bird species, indicating that these trees could function as substitute resources in altered habitats (Zapponi et al. 2014). This pattern is not exclusive and has also been observed, albeit to a lesser extent, in other altered ecoregions such as the Atlantic Forest and the Espinal of Buenos Aires Province (Bonaparte et al. 2020, Jauregui et al. 2021). Although this study did not quantify tree availability at the site, evidence from these modified forests in Argentina suggests that the use of exotic species (such as Chinaberry and Eucalyptus) may increase as the availability of suitable native trees decreases. For this reason, it is important to study in-depth the potential role of different native and exotic tree species in a fragmented forest context such as the Espinal.

Regarding cavity type, secondary users showed a proportionally higher use of cavities generated by decay compared with those excavated by woodpeckers, in agreement with what has been reported in other ecoregions of the country (e.g., Yungas, Atlantic Forest, Humid Chaco), where natural decay is the main mechanism of cavity creation used by secondary cavity nesters (Cornelius et al. 2008, Cockle et al. 2011, Schaaf et al. 2020, Di Sallo & Cockle 2022). Additionally, because cavities generated by decay usually reach larger dimensions (e.g., diameter, depth, entrance size) than woodpecker cavities, their greater use by large secondary users may be directly related to these requirements (Schaaf et al. 2020, Di Sallo & Cockle 2022). In the case of excavating birds, these also show specificity, actively selecting mature trees with sufficient diameters and appropriate wood hardness (Jauregui et al. 2021, Di Sallo & Cockle 2025). This is relevant because mature trees (both living and standing dead) are often removed early in the forest intervention cycle (Manning & Lindenmayer 2009, Schaaf et al. 2021).

The results of this study, based on natural history data collected over decades, may be crucial for the design of conservation and environmental education strategies in the Espinal and other ecoregions facing similar anthropogenic pressures. The presence of exotic trees used by birds could provide an opportunity for the creation of biological corridors or supplementary habitats (Bonaparte et al. 2020, Jauregui et al. 2021, Ossi et al. 2022), but it is essential to better understand the effect of these trees on the ecological dynamics of native forests. Monitoring cavity dynamics and their use by birds in landscapes with different degrees of anthropogenic modification could provide key information to better understand the resilience of bird species to landscape change.

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## SUPPLEMENTARY MATERIAL

You can access the supplementary material for this article by visiting the link: https://doi.org/10.56178/eh.v41i1.1528.

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# ENDOCRANIAL ANATOMY OF THE FOSSIL FURNARIID *Pseudoseisura cursor* (AVES, PASSERIFORMES): PALEOECOLOGICAL PERSPECTIVES AND EVOLUTIONARY IMPLICATIONS

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**ABSTRACT:** Furnariidae is a family endemic to the Neotropics and is one of the most diverse families of Passeriformes, and although it is one of the Neotropical families with the best fossil record, in Passeriformes in general the fossil record is scarce, which can make it difficult to interpret the evolution of the order in general. *Pseudoseisura cursor*, from the Ensenadan (Early–Middle Pleistocene) of Buenos Aires Province, Argentina, is considered the sister taxon of the extant species of the genus. This study describes the endocranial anatomy of this species and compares it with that of other extant Furnariidae to infer ecological aspects. A 3D model of the endocranium (i.e., a proxy for the brain) was created from micro-CT scans obtained from the holotype, which was described and measured (linear and surface-based measurements). Its body mass and endocranial volume were calculated, as well as its auditory capacities. Compared to the Brown Cacholote (*Pseudoseisura lophotes*), the endocranium of *P. cursor* shows general similarities but presents specific differences, such as greater dorsoventral development of the Wulsts and longer olfactory bulbs and flocculi, possibly related to its ancestral condition or functional adaptations. Although *P. cursor* had a greater body mass relative to the Brown Cacholote, its brain was proportionally smaller, with a volume of 9.73 times its body mass (23.59 times in the Brown Cacholote), which could be linked to the trend of body size reduction in extant species and the functional modularity of the brain. Additionally, *P. cursor* exhibited auditory capacities similar to those of Rufous Hornero (*Furnarius rufus*) and Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), possibly due to a similar habitat.

**KEYWORDS:** *evolution, Furnariidae, micro-CT, neuroanatomy, paleobiology, paleoecology*

Furnariidae corresponds to one of the most diverse families of Passeriformes within the order in the Neotropics (Winkler et al. 2020), including, to date, 318 described species, among which horneros and thornbirds stand out. It inhabits all types of environments, from deserts to tropical forests throughout the continent (Fjeldså et al. 2005). Their nests are usually complex and elaborate, a distinctive trait of the group (Olson 2001, Irestedt et al. 2006, Winkler et al. 2020). Most members of the family feed on insects and other small arthropods that they capture mainly from leaves or from the surface of trunks or by scratching the leaf litter (Ohlson et al. 2008, Winkler et al. 2020). Some species may feed on small vertebrates, such as frogs and lizards (Winkler et al. 2020), or include seeds and fruits in their diet (Lopes et al. 2003, Winkler et al. 2020).

Within this family, the genus *Pseudoseisura* groups species adapted to open or semi-open environments with xerophilous arboreal or shrubby vegetation. These furnariids are fundamentally terrestrial, as the

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prolonged daily activity of searching for food is carried out on the ground. The White-throated Cacholote (*Pseudoseisura gutturalis*) is the species that spends the most time on the ground and runs more easily than its congeners (Ridgely & Tudor 1994), whereas the more northerly species, the Brown Cacholote (*Pseudoseisura lophotes*) and the Caatinga Cacholote (*Pseudoseisura cristata*), are somewhat more arboreal, swaying abruptly while walking. Due to their nesting habits, the three species are closely associated with environments containing thorny trees or shrubs, being recognized in the ornithological literature as 'exaggerated thornbirds' (Ridgely & Tudor 1994), owing to these habits and their large body size (Tonni & Noriega 2001).

Paradoxically, despite their high diversity and abundance, the fossil record of Furnariidae is scarce compared to other groups of birds. Nevertheless, within Passeriformes, this family has a considerable record (Tonni 1977, Noriega 1991, Claramunt & Rinderknecht 2005, Tambussi 2011, Stefanini et al. 2016, Nascimento & Silveira 2024), although still insufficient to accurately reconstruct its evolutionary history (Noriega 1998). *Pseudoseisura cursor* (Fig. 1) (Furnariidae) is a fossil species that comes from the Ensenadan (Early–Middle Pleistocene) of Buenos Aires province, Argentina. Tonni & Noriega (2001) consider this fossil taxon to constitute the sister group of the extant species of the genus (Fig. 2); however, it is important to emphasize that the phylogenetic position of *P. cursor* is far from being considered established, since its position has not been rigorously tested. The events that gave rise to the genus *Pseudoseisura* would have begun during the glacial maximum following the late Ensenadan (after 1.0–0.9 Ma), coinciding with arid climatic conditions (Tonni & Noriega 2001). The material described by Tonni & Noriega (2001) consists of incomplete cranium and mandible; incomplete left humerus, distal extremity of right humerus; right and left carpometacarpus; left ulna, incomplete right ulna; right radius; phalanx 1 of wing digit II; incomplete left and right coracoids; incomplete sternum; incomplete left femur; left tibiotarsus; left tarsometatarsus; incomplete pelvis; and pygostyle. All belong to a single individual. In recent years, there has been renewed interest in understanding the early evolution of birds. However, the evolutionary history of their brain and sensory organs still presents numerous unanswered questions (Kurochkin et al. 2007). Endocasts of the neurocranium constitute fundamental tools to unravel this history, since they allow, through various quantitative and qualitative analyses, comparison of the size and shape of the brain of extinct species with extant ones, evaluating the degree of encephalization and its correlation with ecological habits (Jerison 2006). The application of endocranial models as proxies of brain structures allows, even in the absence of preserved brain tissue, the establishment of functional comparisons between fossil and extant species. This methodology has proven effective in previous studies on sensory and ecological evolution in birds (Witmer et al. 2008, Early et al. 2020).

There is broad consensus regarding the significant correlation between brain size and the development of cognitive abilities in vertebrates (Møller 2010). This relationship suggests that brain size directly influences behavior, which has important implications for ecological and evolutionary processes (Dukas 2004). It has been demonstrated that more developed brain areas are associated with increased information-processing capacities of those areas (Brenowitz & Arnold 1986, Iwaniuk & Wylie 2006). In the case of birds, the study of brain anatomy through computed tomography has revealed a direct relationship between the size and shape of brain regions and the structures of the endocranium (Early et al. 2020), understood as the

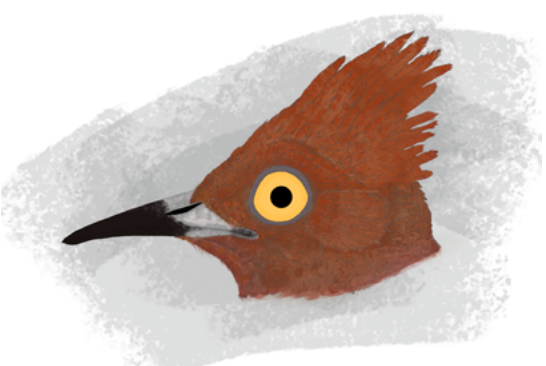

**Figure 1.** Illustration of the external appearance of *Pseudoseisura cursor*, based on skull morphology. Digital reconstruction by doctoral candidate Jesús María Dorado.

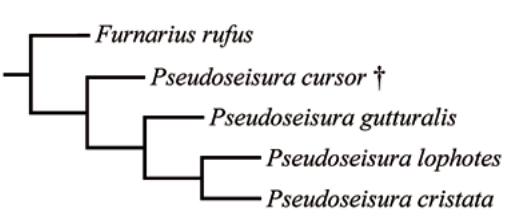


**Figure 2.** Phylogenetic tree of *Pseudoseisura* species. The Rufous Hornero (*Furnarius rufus*) represents the outgroup. Figure taken and modified from Tonni & Noriega (2001). It should be noted that this is only a proposal, and that in the absence of other studies evaluating the phylogenetic position of the fossil taxon, alternative hypotheses cannot be ruled out.

internal surface of the skull that contains and protects the brain. This allows inference of the sensory and motor capacities of different groups of birds from the analysis of endocranial models, regardless of the presence of the brain (Witmer & Ridgely 2008, Tambussi et al. 2014, 2015). During embryonic development, the interaction between the brain and the bony material produces an interface surface that exactly replicates the surface of the brain and that, in many fossil specimens, is preserved and can be studied through casts or digital models (Balanoff & Bever 2017). Therefore, the endocranial cast is an excellent proxy for studying the brain surface of birds (Early et al. 2020).

Within this framework, the main objective of this study was to estimate possible life habits of *P. cursor* based on the description of its endocranial cast and its comparison with the endocranial casts of other furnariids. Under the premise proposed by Tonni & Noriega (2001) regarding the close relationship of this fossil taxon with extant species of the genus, and considering that extant species of *Pseudoseisura* show significant ecological and behavioral similarities—such as preference for semiarid environments, terrestrial behavior, and similar vocal patterns—it could be assumed that these traits are also reflected in endocranial morphological homologies. Therefore, it is hypothesized that the morphology and relative size of the endocranium of *P. cursor* are similar to those of other species of the genus *Pseudoseisura*, such as the Brown Cacholote, as well as the relative surfaces of the endocranial structures and their auditory capacities.

## METHODS

*Specimens*. The holotype of *Pseudoseisura cursor* MLP-XI-14-1 is housed in the collection of the División Paleontología de Vertebrados of the Museo de Ciencias Naturales de La Plata. For comparisons, data from specimens of the family Furnariidae published in Demmel Ferreira et al. (2024) were used. No live animals were used in this study.

*Processing*. X-ray microtomography of the skull of *P. cursor* was performed using a commercial Bruker Skyscan 1272 system belonging to the Facultad de Odontología de la Universidad de Buenos Aires (FOUBA). The resolution used was 25 µm, with an energy of 100 µA and 100 kV. The resulting DICOM files were processed in the software Avizo (Version 7.1), where anatomical structures were manually segmented and a three-dimensional model of the endocranium was generated.

### Description and measurements

Based on the generated three-dimensional model, a detailed description of the endocranium was carried out, including the inner ear, nerves, and blood vessels. The description follows the anatomical terminology for the central nervous system proposed mainly by Breazile & Kuenzel (1993). The number of cerebellar folds refers only to those exposed. Both linear (Fig. 3A) and surface (Fig. 3B) measurements of the different anatomical structures were taken following Demmel Ferreira et al. (2024). Linear measurements were taken in millimeters using tools in the Avizo software. In order to achieve a better representation of shapes, indices were calculated from the linear measurements. Surface measurements were taken using the software Geomagic Studio (version 2012). These measurements are expressed as percentages relative to the total endocranial surface, in order to provide quantitative information mainly on the size of the different brain structures. Body mass (BM) of *P. cursor* was calculated following the method proposed by Field et al. (2013). According to the authors, the most accurate indicator for estimating body mass in flying birds is the maximum diameter of the humeral articular facet of the coracoid (the glenoid cavity). Field et al. (2013) suggest that, in most cases, this indicator can provide the most accurate estimates of body mass for fossil flying birds. Based on this, the maximum diameter of the articular facet of the right and left humerus of *P. cursor* was measured and both measurements were averaged. The formula indicated in the study was then applied: ln(BM) = 2.44*(lnHAF) + 2.00, where BM is body mass and HAF is the measurement of the humeral articular facet. Brain volume (BV) was calculated using the software Avizo. Hearing range (Hz) and mean hearing (Hz) were calculated following Walsh et al. (2009).

### Estimation of possible habits

The inference of potential behaviors and ecological habits of *P. cursor* was carried out qualitatively, assisted by comparison with extant species of the same genus and of other genera within the same family.

Unless otherwise specified, the terms ‘endocranium’, ‘endocranial cast’, ‘endocranial model’, and derived terms will be used interchangeably to refer to the brain proxy.

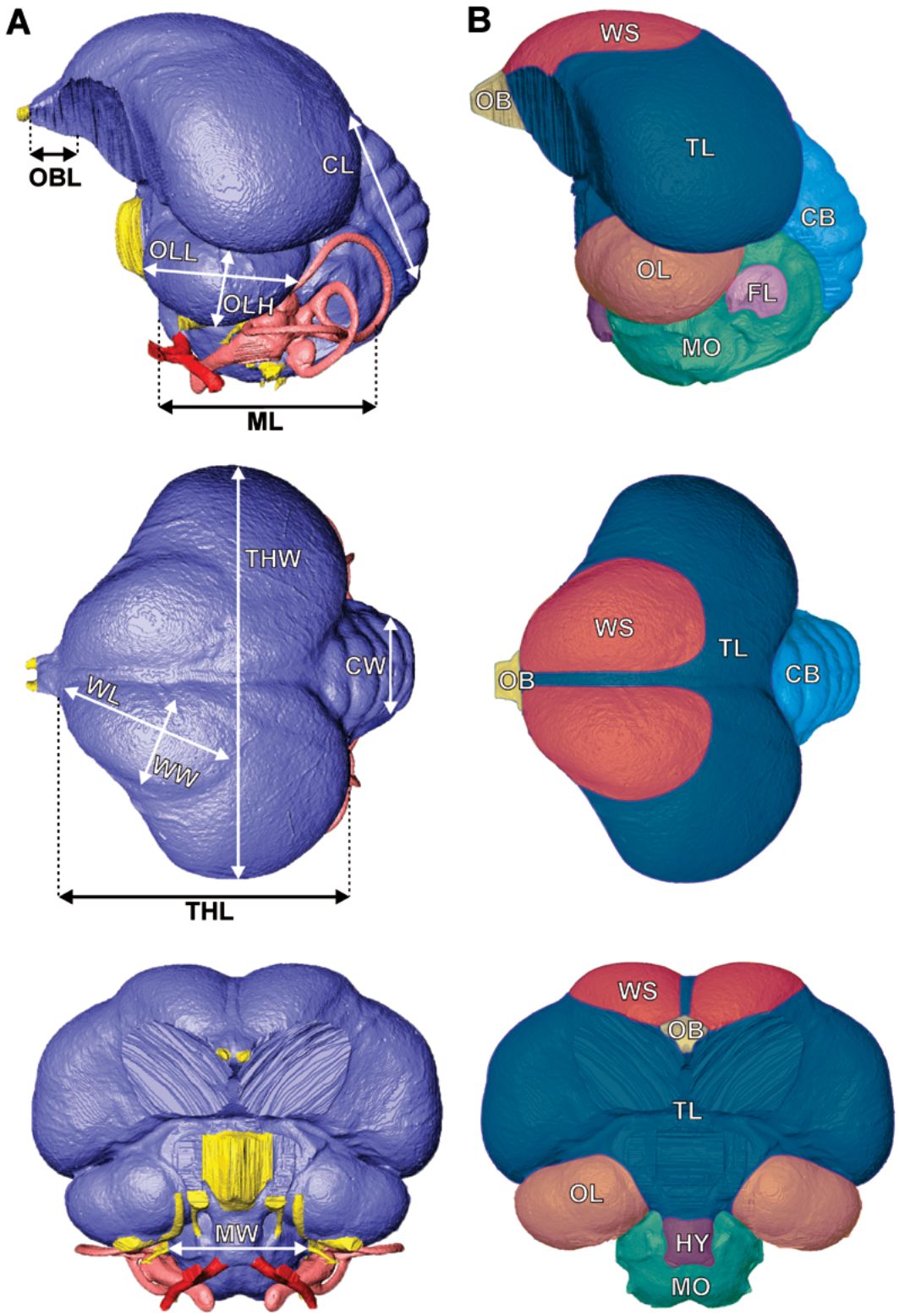


**Figure 3.** Linear and surface measurements taken from the 3D endocranial model of *Pseudoseisura cursor*. Figure taken and modified from Demmel Ferreira et al. (2024). The endocranial model shown in the image belongs to the Great Kiskadee (*Pitangus sulphuratus*). Views: A, linear measurements; B, surface measurements. Abbreviations: CB, cerebellum; CL, cerebellar length; CW, cerebellar width; FL, flocculi; HY, hypophysis; ML, medulla length; MO, medulla oblongata; MW, medulla width; OB, olfactory bulb; OBL, olfactory bulb length; OL, optic lobes; OLH, optic lobe height; OLL, optic lobe length; THL, telencephalic hemisphere length; THW, telencephalic hemisphere width; TL, remaining telencephalon; WL, Wulst length; WS, Wulsts; WW, Wulst width.

## RESULTS

### Anatomical description

The endocranium corresponds to a pneumocephalic brain type (Hofer 1952), which implies that the brain is positioned dorsally to the rostrum and has a marked dorsoventral overlap of the telencephalic hemispheres over the optic lobes and the medulla oblongata (Fig. 4). In dorsal view and in general terms, the endocranium has a subrounded shape (Fig. 4).

*Telencephalon* (Fig. 4): The telencephalon is slightly longer than it is wide (Tables 1 & 2). The hemispheres are domed and pyriform in dorsal view and are mediolaterally expanded. The interhemispheric fissure is wide and deep and is uniform along its entire length. The eminentiae sagittales (Wulsts) correspond to type A (Stingelin 1957), that is, they are positioned rostrally in relation to the length of the telencephalic hemispheres. The Wulsts are elongated and subrounded in shape, and their contact with the interhemispheric fissure is straight, with well-defined margins. The vallecula could not be identified. The olfactory bulb is wide at its origin and narrows rostrally, being conical in shape.

*Diencephalon* (Figs. 4C & D): The hypophysis is wide, robust, and hourglass-shaped in rostral view. The pineal gland could not be identified because it does not leave an impression on the endocranium, as in most birds.

*Mesencephalon* (Figs. 4A, B, C & D): The optic lobes are subspherical and globose in lateral view and are

**Table 1.** Linear measurements in millimeters (mm) of the different anatomical structures of the endocranium.
* Data obtained from Demmel Ferreira et al. (2024).
Abbreviations: CL, cerebellar length; CW, cerebellar width; FL, flocculus length; ML, medulla length; MW, medulla width; OBL, olfactory bulb length; OLH, optic lobe height; OLL, optic lobe length; THL telencephalic hemisphere length; THW, telencephalic hemisphere width; WL, Wulst length; WW, Wulst width.

| Species | TLH | THW | WL | WW | OBL | OLL | OLH | CL | CW | FL | ML | MW |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pseudoseisura cursor* | 16.79 | 21.63 | 13.61 | 8.39 | 2.66 | 6.46 | 4.61 | 7.31 | 5.31 | 3.59 | 8.43 | 6.29 |
| *Cinclodes fuscus* * | 12.28 | 13.99 | 9.97 | 4.37 | 1.22 | 5.85 | 3.24 | 5.84 | 4.68 | 1.26 | 7.33 | 4.61 |
| *Coryphistera alaudina* * | 14.51 | 11.44 | 8.53 | 4.46 | 1.12 | 5.42 | 3.28 | 5.97 | 4.32 | 0.91 | 5.28 | 4.09 |
| *Drymornis bridgesii* * | 17.15 | 20.57 | 13.67 | 7.84 | 1.33 | 6.38 | 3.27 | 8.30 | 4.83 | 1.28 | 7.03 | 5.36 |
| *Furnarius rufus* * | 13.55 | 16.57 | 11.23 | 4.68 | 0.64 | 7.42 | 3.96 | 7.10 | 4.77 | 1.92 | 6.08 | 4.62 |
| *Lepidocolaptes angustirostris* * | 12.06 | 15.72 | 11.06 | 5.81 | 0.74 | 5.91 | 2.77 | 6.72 | 4.81 | 1.54 | 6.09 | 4.58 |
| *Pseudoseisura lophotes* * | 15.38 | 19.30 | 11.20 | 6.12 | 1.15 | 6.16 | 3.71 | 7.41 | 4.99 | 1.50 | 6.67 | 5.66 |
| *Syndactyla rufosuperciliata* * | 14.09 | 16.00 | 9.91 | 5.53 | 1.20 | 5.92 | 3.21 | 7.28 | 4.86 | 1.31 | 6.40 | 4.77 |

**Table 2.** Indices calculated from linear measurements.
* Data obtained from Demmel Ferreira et al. (2024).
Abbreviations: CL, cerebellar length; CW, cerebellar width; FL, flocculus length; ML, medulla length; MW, medulla width; OBL, olfactory bulb length; OLH, optic lobe height; OLL, optic lobe length; THL telencephalic hemisphere length; THW, telencephalic hemisphere width; WL, Wulst length; WW, Wulst width.

| Species | THL/ THW | WL/ WW | OBL/ THL | OLL/OLH | CL/ CW | FL/ CW | ML/ MW |
|---|---|---|---|---|---|---|---|
| *Pseudoseisura cursor* | 0.776 | 1.622 | 0.158 | 1.401 | 1.377 | 0.676 | 1.340 |
| *Cinclodes fuscus* * | 0.878 | 2.281 | 0.099 | 1.806 | 1.248 | 0.269 | 1.590 |
| *Coryphistera alaudina* * | 1.268 | 1.913 | 0.077 | 1.652 | 1.382 | 0.211 | 1.291 |
| *Drymornis bridgesii* * | 0.834 | 1.744 | 0.078 | 1.951 | 1.718 | 0.265 | 1.312 |
| *Furnarius rufus* * | 0.818 | 2.400 | 0.047 | 1.874 | 1.488 | 0.403 | 1.316 |
| *Lepidocolaptes angustirostris* * | 0.767 | 1.904 | 0.061 | 2.134 | 1.397 | 0.320 | 1.330 |
| *Pseudoseisura lophotes* * | 0.797 | 1.830 | 0.075 | 1.660 | 1.485 | 0.301 | 1.178 |
| *Syndactyla rufosuperciliata* * | 0.861 | 1.792 | 0.085 | 1.844 | 1.498 | 0.270 | 1.342 |

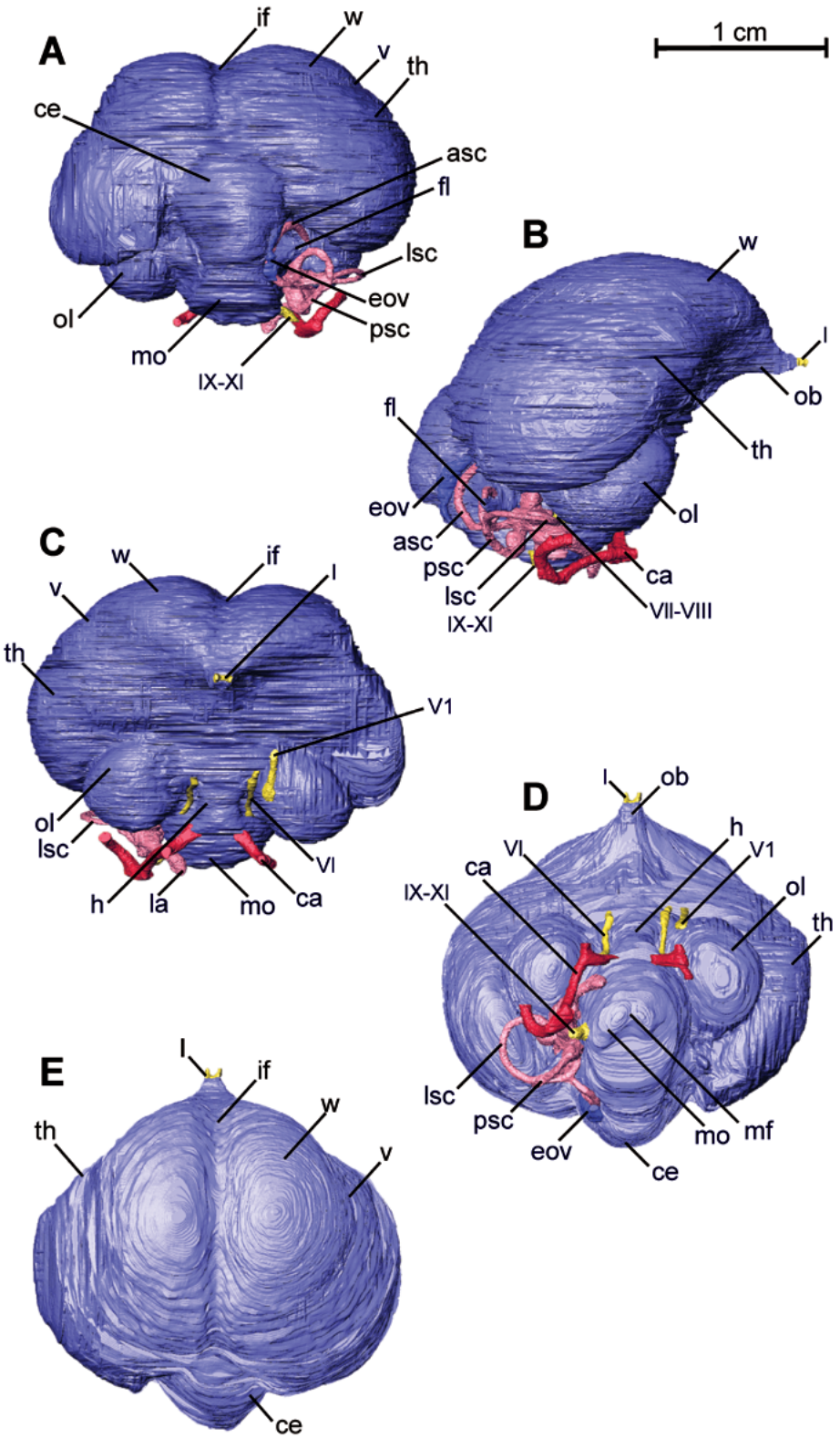


**Figure 4.** Virtual 3D reconstruction of the endocranial cast of *Pseudoseisura cursor* produced from computed microtomography, with anatomical structures indicated. Abbreviations: asc, anterior semicircular canal; ca, carotid; ce, cerebellum; eov, external occipital vein; fl, flocculus; h, hypophysis; I, nerve one; IX–XI, exits of nerves nine to eleven; if, interhemispheric fissure; la, lagena; lsc, lateral semicircular canal; mf, median fissure; mo, medulla oblongata; ob, olfactory bulb; ol, optic lobe; psc, posterior semicircular canal; th, telencephalic hemisphere; v, vallecula; V1, branch one of nerve five; VI, nerve six; VII–VIII, exits of nerves seven and eight; w, Wulst.

positioned rostrally in relation to the caudal limit of the Wulsts. The contact between the optic lobes and the telencephalon forms a line that curves markedly ventrolaterally; therefore, in rostral view they show a dorsoventral orientation. The telencephalic hemispheres 'wrap' the dorsal surface of the optic lobes, as in most Neornithes (Chiappe et al. 2024).

*Metencephalon* (Figs. 4A, B, D & E): The cerebellum is short and wide, and the contact with the telencephalon has the shape of an inverted open 'U'. It was not possible to reconstruct the cerebellar folds due to the state of preservation of the skull. The flocculi are wide at their origin and extend laterocaudally, without curvatures or folds.

*Myelencephalon* (Figs. 4A, C & D): The medulla oblongata is elongated in the rostrocaudal direction. The median fissure is shallow and poorly marked. The medulla has a globose appearance in rostral view.

*Cranial nerves* (Figs. 4A, B, C & D): Due to the state of preservation of the skull, it was not possible to reconstruct all cranial nerves. The olfactory nerve (I) projects rostrally from the olfactory bulb. The origin of this nerve is common to both branches, with the common portion being short and subtle. Of the trigeminal nerve (V), only the ophthalmic branch (1) could be reconstructed; it runs over the medial portion of the optic lobes. This branch is slender, with a rounded cross section. The abducens nerve (VI) originates in the most rostral portion of the medulla and extends dorsorostrally, parallel to branch 1 of nerve V. It is slender and circular in cross section. The facial and vestibulocochlear nerves (VII and VIII) have a shared origin on the lateral sides of the medulla, partially covered by the inner ear. The glossopharyngeal, vagus, and accessory nerves (IX, X, and XI) have a common origin, as in most birds (Breazile & Kuenzel 1993), located in the ventrolateral region of the medulla. The common origin of these nerves is rounded and oval in cross section. The optic (II), oculomotor (III), and trochlear (IV) nerves could not be reconstructed.

*Vasculature* (Figs. 4A, B, C & D): The carotid canals have a subrounded cross section. Both carotids reach the hypophysis independently; therefore, there is no intercarotid anastomosis. The external occipital vein follows the lateral margins of the cerebellum. It is robust and conspicuous in appearance. Due to the state of preservation, it was not possible to identify the occipital sinus.

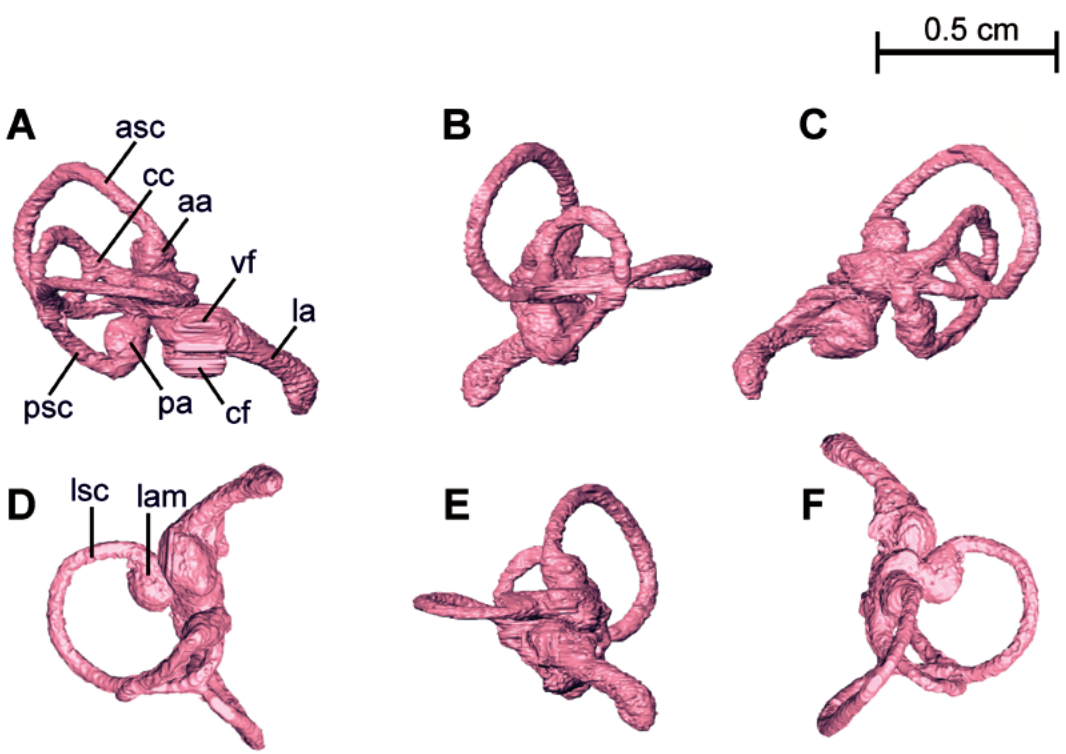


**Figure 5.** Virtual 3D reconstruction of the endocranial cast of the right inner ear of *Pseudoseisura cursor*, with anatomical structures indicated. Abbreviations: aa, anterior ampulla; asc, anterior semicircular canal; cc, common crus; cf, cochlear fovea; la, lagena; lam, lateral ampulla; lsc, lateral semicircular canal; pa, posterior ampulla; psc, posterior semicircular canal; vf, vestibular fovea.

*Inner ear* (Fig. 5): All semicircular canals have a subrounded cross section. The posterior semicircular canal (PSC) is the least developed (i.e., the one with the smallest diameter), whereas the anterior (ASC) and lateral (LSC) canals show similar development. All three ampullae are globose and oriented caudally. The common crus is short and robust and is oriented obliquely relative to the LSC. The lagena curves slightly medially, and its cranial end is oriented ventrally. The vestibular fenestra is oval and conspicuous; it is clearly marked. The cochlear fenestra is smaller than the vestibular one; it is also oval and slightly more elongated.

## DISCUSSION

The proposal of Tonni & Noriega (2001) places this species as the first extinct species of the genus *Pseudoseisura*, and they postulate its condition as the sister taxon of the other species of the genus. When comparing the shape of the endocranium of *Pseudoseisura cursor* (Fig. 4) with that of the Brown Cacholote (Demmel Ferreira et al. 2024), it is possible to state that, in general terms, the endocrania are similar. However, due to the lack of specific and rigorous phylogenetic studies, there is some phylogenetic uncertainty, and therefore the results should be interpreted with the caution that such uncertainty requires. Regarding the linear measurements (Table 1) and the indices of those measurements (Table 2), there are no major differences indicating that the shape of the different anatomical structures varies markedly. By analyzing Table 2, it can be observed that the olfactory bulb of *P. cursor* is considerably longer relative to telencephalon length than in the Brown Cacholote, which could be due to a greater predominance of olfaction in *P. cursor* than in extant furnariids. The flocculi are also longer relative to cerebellar width in *P. cursor* than in the Brown Cacholote. This could be explained by an increase in neuronal density in specific regions, which facilitates the incorporation of additional brain pathways or the elaboration or increased acuity of existing pathways (Ksepka et al. 2020). Some authors suggest that there is differential growth of individual brain regions, which could be divided into distinct functional regions, indicating a certain degree of modular evolution (Iwaniuk et al. 2004, 2005, Healy & Rowe 2007, Balanoff et al. 2016, Smaers & Vanier 2019).

When analyzing the relative percentages of surface measurements (Table 3), it can be observed that the Wulsts represent more than twice the surface occupied by the optic lobes. This comparison is made because the Wulsts (histologically corresponding to the hyperpallium) process visual information (caudal region) and somatosensory information (rostral region) (Atoji et al. 2016). This could indicate that both vision and somatosensory information were of great importance. The amount and type of information received by the Wulsts is closely linked to both locomotor and trophic habits (Wylie et al. 2015, Stacho et al. 2020). This, together with the idea of a highly cursorial locomotor habit (Tonni & Noriega 2001), could indicate it foraged on the ground, searching for

**Table 3.** Surface measurements expressed as percentages (%) relative to the total endocranial surface.
* Data obtained from Demmel Ferreira et al. (2024).
** Structure that could not be reconstructed in the endocranial model.

| Species | Wulsts | Olfactory bulb | Hypophisis | Optic lobes | Cerebellum | Flocculi | Medulla | Optic chiasm | Remaining telencephalon |
|---|---|---|---|---|---|---|---|---|---|
| *Pseudoseisura cursor* | 19.88 | 1.03 | 1.16 | 9.97 | 5.59 | 2.26 | 7.38 | ** | 52.73 |
| *Cinclodes fuscus* * | 14.71 | 1.23 | 1.01 | 16.73 | 6.07 | 2.69 | 11.81 | 0.87 | 44.89 |
| *Coryphistera alaudina* * | 15.30 | 1.01 | 1.12 | 13.05 | 6.20 | 2.20 | 11.91 | 1.08 | 48.14 |
| *Drymornis bridgesii* * | 20.01 | 1.11 | 0.82 | 9.15 | 5.73 | 1.12 | 10.78 | 0.80 | 50.48 |
| *Furnarius rufus* * | 14.51 | 0.86 | 1.17 | 13.93 | 6.57 | 2.62 | 12.10 | 1.26 | 46.98 |
| *Lepidocolaptes angustirostris* * | 19.59 | 1.01 | 0.89 | 11.56 | 7.14 | 2.32 | 11.42 | 0.69 | 45.37 |
| *Pseudoseisura lophotes* * | 17.65 | 0.59 | 0.85 | 11.83 | 6.06 | 2.08 | 12.04 | 0.91 | 47.99 |
| *Syndactyla rufosuperciliata* * | 19.02 | 1.05 | 0.94 | 9.60 | 7.38 | 2.03 | 10.22 | 0.85 | 48.89 |

food among grass or leaf litter. When comparing Wulst and optic lobe values with those of other furnariid species, the Scimitar-billed Woodcreeper (*Drymornis bridgesii*) shows the most similar values, and although this species also feeds on tree trunks and branches, it primarily forages on the ground (Belton 1984, Kratter et al. 1993, Juárez 2021). The Buff-browed Foliage-gleaner (*Syndactyla rufosuperciliata*) also shows similar values, but this species has different foraging behaviors, as it searches for food mainly in the understory, occasionally extending into the canopy and only rarely on the ground. It collects items from branches, dead leaves, and other debris; occasionally it hammers branches (Remsen 2020). In this case, it is likely that the similarity in Wulst surface values is more related to the processing of sensory information. The cerebellar surface value of *P. cursor* is striking when compared with the other species: it is the smallest value, and the closest value is the one that corresponds to the Scimitar-billed Woodcreeper. Cerebellar size is strongly linked to the size of the different folds or folia, which in turn are related to different functions and different habits (Sultan & Glickstein 2007). Walsh et al. (2013) recognize that a large cerebellum may have contributed to flight capability, as well as to all modes of avian locomotion. Hall et al. (2013) found a positive correlation between the degree of folding of the cerebellar cortex and nest complexity. This suggests that a cerebellum with a higher degree of folding allows greater neuronal density (especially of Purkinje cells), better fine motor processing, and possibly greater learning capacity and motor sequencing. Given that the cerebellum is also involved in fine motor control (Hall et al. 2013), this can influence both flight performance (for example, in precise maneuvers or flight in complex environments such as dense forests) and swimming (Balanoff et al. 2016), or even the construction of complex nests. In the case of *P. cursor*, the

**Table 4.** Body mass in grams (g) and endocranial volume in cubic millimeters ($mm^3$).
* Data obtained from Demmel Ferreira et al. (2024).
** According to the formula used (Field et al. 2013), the mean percent prediction error is 12.95, and the 95% confidence interval of the percent prediction error is 1.07.
Abbreviations: BM, body mass; EV, endocranial volume.

| Species | Body mass | Endocranial volume | EV/BM |
|---|---|---|---|
| *Pseudoseisura cursor* | 262.52** | 2554.99 | 9.73 |
| *Cinclodes fuscus* * | 30.00 | 804.49 | 26.82 |
| *Coryphistera alaudina* * | 30.00 | 809.48 | 26.98 |
| *Drymornis bridgesii* * | 94.00 | 2181.33 | 23.21 |
| *Furnarius rufus* * | 43.70 | 1130.25 | 25.86 |
| *Lepidocolaptes angustirostris* * | 31.50 | 931.45 | 29.57 |
| *Pseudoseisura lophotes* * | 72.40 | 1707.83 | 23.59 |
| *Syndactyla rufosuperciliata* * | 25.60 | 1157.94 | 45.23 |

**Table 5.** Frequencies and hearing ranges expressed in Hertz (Hz).
* Data obtained from Demmel Ferreira et al. (2024).

| Species | Optimal frequency | Mean frequency | Minimum frequency | Maximum frequency |
|---|---|---|---|---|
| *Pseudoseisura cursor* | 5385.80 | 3138.62 | 445.72 | 5831.52 |
| *Cinclodes fuscus* * | 5617.83 | 3264.49 | 455.57 | 6073.41 |
| *Coryphistera alaudina* * | 6176.63 | 3567.61 | 479.30 | 6655.93 |
| *Drymornis bridgesii* * | 4476.19 | 2645.20 | 407.11 | 4883.30 |
| *Furnarius rufus* * | 5448.09 | 3172.41 | 448.37 | 5896.46 |
| *Lepidocolaptes angustirostris* * | 5190.04 | 3032.43 | 437.41 | 5627.45 |
| *Pseudoseisura lophotes* * | 4944.42 | 2899.20 | 426.99 | 5371.41 |
| *Syndactyla rufosuperciliata* * | 4954.19 | 2904.50 | 427.40 | 5381.59 |

relatively small cerebellar surface compared to other furnariids could be related to a lifestyle less demanding in terms of fine motor skills and behavioral complexity. It may have inhabited more open or less structurally complex areas, perhaps with a more terrestrial lifestyle or less dependence on flight, or it may not have built highly complex nests. It is also important to mention that the low relative surface values for the cerebellum could be due to limited space within the skull, in which some structures increase their surface area at the expense of others, or to a phylogenetic constraint.

A striking aspect of the relative surface values is that those of *P. cursor* are considerably different from those of the species of the same genus, the Brown Cacholote. Although the values of the species considered here do not show large variation, it is possible to state, as shown above, that there are species with values more similar to *P. cursor* than the Brown Cacholote. Again, this could be due to ancestral conditions of the fossil species. A comparison with the other members of the *Pseudoseisura* clade would be interesting in order to obtain a more complete picture.

Regarding the relationship between relative endocranial volume and body mass (in which *P. cursor* showed a smaller value than other Furnariidae; Table 4), Ksepka et al. (2020) propose that the trend toward relatively larger brain sizes along the phylogeny was driven by selection for smaller body sizes. Evolutionary rates appear to have stabilized over time, while directional selection acted on individual clades. Although body size is a possible explanation for variation in relative brain size, some authors suggest that high levels of encephalization could be due to differential growth of individual brain regions, which could be divided into distinct functional regions, indicating a certain degree of modular evolution (Iwaniuk et al. 2004, 2005, Healy & Rowe 2007, Balanoff et al. 2016, Smaers & Vanier 2019). This may be linked to ancestry and could indicate, as proposed by Ksepka et al. (2020), that extant furnariids experienced a more pronounced decrease in body mass than in endocranial volume, compared to fossil species. It is worth mentioning that the body mass estimate of *P. cursor* is unprecedented prior to the publication of this work and represents a novel result in itself. Although the calculated value is striking in relation to the body mass of other furnariids, it is currently the estimate that provides the greatest precision for this parameter (Field et al. 2013). Tonni & Noriega (2001) described *P. cursor* as a large species, at least 'larger than the three known species of *Pseudoseisura*', so the body mass value could be consistent with that idea.

With respect to hearing, the Acoustic Adaptation Hypothesis (AAH) proposes that habitat structure has shaped the evolution of the acoustic properties of bird songs (and therefore hearing; Morton 1975, Hansen 1979, Boncoraglio & Saino 2007). Warm, dry air improves sound transmission (Harris 1966, Michelsen & Larsen 1983), whereas dense foliage increases attenuation (Aylor 1972, Martens 1980). Tonni & Noriega (2001) infer that *P. cursor* inhabited open or semi-open Chaco-type environments, where sound would have been transmitted without major difficulties. The auditory capabilities of *P. cursor* (Table 5) showed intermediate values within the comparative framework, and its optimal hearing frequency is close to that of the Rufous Hornero (*Furnarius rufus*) and the Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*). This may be explained by the fact that the Rufous Hornero inhabits a variety of open habitats: disturbed areas with bare ground, secondary scrub, grasslands, and agricultural lands, as well as urban parks and gardens (Remsen & Bonan 2020), showing some similarity to the habitat proposed for *P. cursor*. The latter occurs in slightly more vegetated habitats, such as open forests, scrublands, and savannas (Marantz et al. 2020). These similarities in habitat types could explain the similarity in hearing frequencies among *P. cursor*, the Rufous Hornero, and the Narrow-billed Woodcreeper. The reason why the Brown Cacholote has lower hearing frequencies than *P. cursor* could be due to the fact that this species inhabits different types of habitats (mainly tropical deciduous forests, forest edges, and secondary scrub, among other forested environments; Remsen 2024), which differ from those proposed for the fossil species. According to the AAH, different habitats imply different acoustic properties. The meta-analysis carried out by Boncoraglio & Saino (2007), while supporting the AAH, warns that habitat structure only weakly predicts the acoustic properties of bird songs. Therefore, other potentially relevant factors should be included in realistic models of the evolution of avian song acoustics.

In conclusion, there are strong similarities in the general morphology of the endocranium of *P. cursor* compared to other furnariids. However, it is important to emphasize that, to date, there are no specific and rigorous phylogenetic studies regarding its assignment to the genus *Pseudoseisura*; therefore, alternative hypotheses of its affiliation cannot be ruled out, and the results presented here should be interpreted with appropriate caution. Analysis of its endocranial anatomy allows inference of a strong predominance

of olfaction in *P. cursor* compared to extant furnariids, accompanied by a notable relevance of vision and somatosensory information. These traits are related both to its cursorial locomotion (Tonni & Noriega 2001) and to its trophic habit, indicating that foraging occurred on the ground, among grass or leaf litter. From the relative surface of the cerebellum, it can be inferred that it may have had a lifestyle less demanding in terms of fine motor skills and behavioral complexity, more terrestrial or with less dependence on flight, and perhaps did not build highly complex nests. Analysis of the auditory range suggests that this species primarily inhabited open or semi-open Chaco-type environments, more open or less structurally complex areas, in agreement with Tonni & Noriega (2001). The remarkable preservation of the brain and skull of *P. cursor*, together with its age of approximately 2.5 million years and its taxonomic position, make it a key specimen within the fossil record of Neotropical birds, especially of Passeriformes, the avian group with the greatest biodiversity.

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# HAND REARING OF THE HOODED GREBE (*Podiceps gallardoi*) AND THE SILVERY GREBE (*Podiceps occipitalis*) AS A FUNDAMENTAL RECOVERY STRATEGY FOR A CRITICALLY ENDANGERED SPECIES

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**ABSTRACT:** Habitat loss, climate change, and invasive alien species have led the critically endangered Hooded Grebe (*Podiceps gallardoi*) to decline by 80% of its population. The Silvery Grebe (*Podiceps occipitalis,* least concern), is a closely related species that can be used as a biological proxy. As a complement to the *in situ* conservation actions developed over the past decade to protect the Hooded Grebe, we proposed hand rearing as part of the conservation strategy, given that in 97.4% of clutches, the nesting pairs abandon the second egg. Given the limited information regarding captive rearing of grebes, we evaluated variables that could affect hatching success and chick survival, including incubation stage at collection, transportation duration, temperature-humidity incubation protocol, daily egg-weight loss, and care (feeding and swimming) frequency. We collected and artificially incubated eggs from Hooded Grebes and Silvery Grebes for four breeding seasons. We achieved a 73% hatching success rate. The longest Hooded Grebe chick survival was 144 hours, and we successfully raised a Silvery Grebe fledgling, which was released into the wild after 67 days. Transportation duration, daily egg-weight loss, and incubation protocol did not affect hatching success. Eggs collected in the later stages of incubation had a higher hatching rate. We observed a higher survival time associated with the high-temperature and humidity incubation protocol. Chicks hatched from eggs with a daily egg-weight loss of more than 1% showed higher survival. This was also observed in chicks with more assiduous care. We have defined an appropriate incubation protocol for the Hooded Grebe. In the future, we will focus on determining the appropriate frequency of care and diet. The low reproductive success of the Hooded Grebe in the last years urges the need for actions aimed at increasing annual population recruitment.

**KEYWORDS:** *captive breeding, ex situ management, Hooded Grebe, Podiceps gallardoi, Podiceps occipitalis, reproductive biology, Silvery Grebe*

The grebes (Podicipediformes) are one of the taxonomically of birds of greatest conservation concern, indeed three of the 23 species have been declared extinct in the last three decades, and five others are currently threatened (BirdLife International 2023). Furthermore, habitat alteration, pollution, the introduction of non-native species, and climate change can cause the rapid decline of a species (Winkler et

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al. 2020). The Hooded Grebe (*Podiceps gallardoi*) is an endemic breeding bird of Santa Cruz Province, Argentina, where it breeds in highland lakes on basaltic plateaus in the western part of the province. During winter, Hooded Grebes migrate to the Atlantic Coast estuaries of the Coyle, Gallegos, and Chico-Santa Cruz rivers (Imberti et al. 2020). In the early 1980s, the Hooded Grebe population was estimated to be 3000-5000 individuals (Fjeldså 1986, Beltrán et al. 1992). Counts conducted between 2010 and 2011 showed that in 25 years the population suffered an 80% decrease and an increase in its threats (invasive alien species and loss of reproductive sites due to climate change), with only c. 800 individuals left (Roesler et al. 2012). Consequently, the species was categorized globally as Critically Endangered in 2012 (BirdLife International 2023). In Argentina, it is also considered critically endangered (MAyDS y AA 2017). The causes of decline include predation of adults and juveniles by the invasive American Mink (*Neovison vison*), the destruction of colonies by the Kelp Gull (*Larus dominicanus*), and competition with Rainbow Trout (*Oncorhynchus mykiss*), which has been introduced in some lakes (Roesler et al. 2012, Lancelotti et al. 2017, Fasola & Roesler 2018). In addition, climate-related factors, such as the decrease in precipitation during winter (snowfall) and an increase in wind speed, cause the lakes to dry up (Lancelotti et al. 2020), affecting the viability of reproductive colonies.

The Silvery Grebe (*Podiceps occipitalis*) is evaluated globally as Least Concern because this species has an extremely large range and a large population size. However, the overall population trend is decreasing, and the trend of some of its populations is unknown (BirdLife International 2023). In Argentina, it is considered not threatened (MayDS y AA 2017). This is a closely related species with similar life history to the Hooded Grebe and inhabits the same environments in austral Patagonia (Fjeldså 1983). For this reason, the threats facing the species could be similar. In addition, Hooded and Silvery Grebes frequently form mixed colonies, so any information generated from one species could help to understand the other.

*Ex situ* management has been used to benefit the conservation efforts of threatened species. Species extinctions have been prevented, and for an increasing number of species, conservation restorations or introductions have followed periods of *ex situ* management (IUCN/SSC 2014). Artificial incubation of eggs removed from the wild, hand rearing of chicks, and the subsequent return of birds into their native habitat have been incorporated into the overall recovery strategy for endangered species such as the Mauritius Kestrel (*Falco punctatus*, Jones et al. 1995), the Mauritius Fody (*Foudia rubra*, Cristinacce et al. 2008), the California Condor (*Gymnogyps californianus*, Kuehler & Whitman 1988), and the Hawaiian Crow (*Corvus hawaiiensis*, Kuehler et al. 1994). Nevertheless, *ex situ* breeding experiences in grebes are anecdotal. Between 1924 and 1933, the German biologist Oskar Heinroth attempted several times to breed individuals of Great-crested Grebe (*Podiceps cristatus*) but was never able to get the chicks to survive beyond four days (Hick 1966). Following his example, Hick (1966) artificially incubated eggs of the same species in 1962 and obtained chicks that also died on the fourth day of life. However, in 1963, he managed to breed two individuals until fledgling, whose survival age is not specified. Also working with *Podiceps cristatus*, Kop (1972) collected and artificially incubated five eggs from the field, all five hatched and two individuals lived 11 days, and three individuals lived 61, 72, and 73 days. Herman artificially incubated three *Aechmophorus occidentalis* eggs in 1974 and collected three chicks in the field. The six chicks were satisfactorily reared until at least four months of age, two were released at the age of 14-15 months (MacVean 1988). Ratti successfully reared seven *Aechmophorus clarkii* from eggs collected in the field to 9-12 weeks of age in 1977 (MacVean 1988). Nuechterlein (1981) incubated two abandoned eggs of the Hooded Grebe after the hatching of the first chick and managed to hatch one of them, which survived up to the age of four days. In 1986, within the framework of a plan to conserve the currently extinct *Podilymbus gigas*, MacVean (1988) successfully reared five individuals of *Podilymbus podiceps* from 20 eggs collected in the field and artificially incubated them, obtaining chicks that were two, 20, and 60 days old, and 14-16 months old. In this last case, the strategy appeared to have extremely high potential, however, unfortunately, it was not continued, and the species became extinct (Hunter 1988). Some of these articles do not provide a detailed description of the work methodology. Others are highly detailed, but they are not suitable for working with species from habitats quite different from those of the Hooded Grebe. In any case, they provide the basis for creating experimental work protocols for other species of grebes.

Since 2011, the 'Hooded Grebe Project' (Aves Argentinas / BirdLife International) has been performing *in situ* efforts to conserve the Hooded Grebe population in the short term (Roesler et al. 2018). This project includes actions to protect the colonies by the 'colony guardians' (i.e., specialized technicians who

camp at the colonies to watch and protect the nest from predators; see Roesler et al. 2016). In addition, there is a component of invasive alien species control aimed at preventing depredation of adults, maximizing seasonal recruitment, and restoring reproductive sites (Roesler et al. 2018). These efforts have been successful in halting the population decline; however, due to the low reproductive success of recent seasons, the population is declining again (Roesler et al. 2025).

As a complement to *in situ* actions, we proposed a long term strategy of hand rearing individuals from 'ecologically lost' eggs (i.e., eggs that do not hatch in the wild). This is possible because of the unique life tactic of the Hooded Grebe compared to other grebes (Fjeldså 1986), as 97.4% of breeding pairs raise only one chick and abandon the second egg after the first chick hatches (Roesler 2016). Hand rearing the second egg and releasing individuals may duplicate the recruitment per season. Furthermore, several colonies are destroyed by strong winds, so recovering the eggs before this happens could help mitigate their effect. In addition, given the precarious state of other grebe species, the development of *ex situ* breeding techniques might be helpful in future population recovery efforts.

Our goal is to generate theoretical and practical knowledge for the development of a hand rearing program for the Hooded Grebe, aiming to increase the number of young that survive until migration (i.e., enhance season recruitment) by recovering ecologically lost eggs. Due to the low reproductive success of the species in recent years, we used the Silvery Grebe as a proxy when there was a lack of Hooded Grebe eggs. Our research objectives were to develop a method for obtaining chicks from eggs collected on the lakes, encompassing egg collection, transportation, incubation, and hatching. Additionally, to create a protocol for hand rearing the chicks until they are fledglings, including environmental, management, and feeding variables.

To evaluate the effect on hatching, we compared the incubation period, considering the eggs' collection time, transportation duration between lakes and the hand rearing facilities, five incubation protocols (varying by temperature and humidity), and daily egg-weight loss during artificial incubation. To assess the factors influencing chick survival time, we analyzed the five incubation protocols, variations in daily egg-weight loss during incubation, food options, and the frequency of chick feeding and swimming periods. Here, we present results from initial trials in rearing the critically endangered Hooded Grebe and Silvery Grebe, along with an evaluation of variables affecting hatching success and chick survival for both species.

## METHODS

### Study Area

Between 2015 and 2020, we worked in the breeding area of the Hooded Grebe in western Santa Cruz Province, Patagonia, Argentina, particularly on the plateaus of Lake Buenos Aires and Lake Strobel (Fig. 1). We were able to work in four breeding seasons (December–April), given that breeding colonies were not present in some years. The first rearing facility was located at Estancia Laguna Verde Fishing Lodge (48°30'S, 71°14'W), in the central area of the Strobel Lake Plateau, where we were situated in a container with a large thermal range. We reared grebes there during three seasons (2015–2016, 2016–2017, 2017–2018). In our last season (2019–2020), we developed a fully equipped hand rearing station at Juan Mazar Barnett Biological Station (JMBBS - Aves Argentinas; 47°14'S, 71°11'W). This place was conditioned with thermal isolation on the roof and walls, which allowed ambient temperature to be stable between 15-20°C. This was a significant improvement to the operation of the incubators. We collected eggs of Hooded Grebe and Silvery Grebe in five lakes: Rodríguez 9, Rodríguez 19, LA4 (Buenos Aires Lake Plateau, Fig. 1B), and Ocho and Nueve (Strobel Lake Plateau, Fig. 1C).

### Collection and transportation of eggs

As part of the Hooded Grebe Project, we monitored the lakes where colonies may form every breeding season, looking for nests. When we locate a colony, a 'colony guardian' stays at the site to protect and record the date the eggs are laid (i.e., when eggs are visible on the nest), marking the start of incubation. For hand rearing, we tried to collect eggs after more than 15 days of natural incubation, but if there's a risk of losing the eggs due to a windstorm, we gather them earlier.

To collect the eggs, we used an inflatable boat with oars for two people (Roesler 2016). One person rowed while the other took the eggs from the nest (Fig. 2A). We collected one of the two eggs from each nest. Approaching the colony was always against the wind and never took more than 10 min. All colonies were monitored before and after collection to detect any potential adverse effects of our intervention, and colony reproductive success did not vary. We transported the eggs in thermally insulated boxes with a heat source (hot-water bottles at 55-60°C), which were isolated from the eggs with cotton. With this range of

water temperature, we kept the internal temperature of the box between 25 and 30°C throughout the trip. Eggs were then classified according to the transportation time (from the lake to the breeding center) and the incubation stage at the time of collection. We defined three groups based on transportation duration: <1 h, 1–3 h, and >3 h. We also defined three groups of incubation stages (1–7 days, 8–14 days, 15–21 days) based on the typical incubation period of the Hooded Grebe (20–21 days; Roesler 2016), and we assumed the same period for the Silvery Grebe. We based the assignment of laying dates in some cases on information from direct observation obtained by 'colony guardians', when the colony was found before the eggs were laid. In others, this was estimated by the dates of the lakes' monitoring (i.e., the lake was visited and there was no colony, and subsequently, during monitoring, a colony was found) and the number of days of artificial incubation of the eggs until hatching. In this case, we consider the laying date to be 21 days before the hatching day, although transport and artificial incubation may lengthen the hatching time.

### Artificial egg incubation

Once at the rearing facilities, we marked the eggs with an identification number using a pencil on the shell, weighed them, and placed them horizontally in an incubator (Fig. 2B). After 12 hours, we candled the eggs to check their viability and measured them (length and width). We waited 12 h until then to let the eggs stabilize after the transport. If any non-viable egg is found, it is discarded, but this was not the case.

We tested five temperature/humidity protocols applied to the different egg batches obtained per season. Due to the variability in the number of nests between seasons, it was impossible to maintain a balanced treatment. We started with a standard incubation protocol used in domestic poultry species, which works well in many nondomestic species (Gage & Duerr 2007): high temperature-high humidity (37.1-37.5°C/65-70%; $n$ = 12) in the season 2015/2016. Due to the low survival time of Hooded Grebe chicks, we hypothesized that a colder incubation temperature could increase incubation time and thus produce stronger chicks. Therefore, in the next season

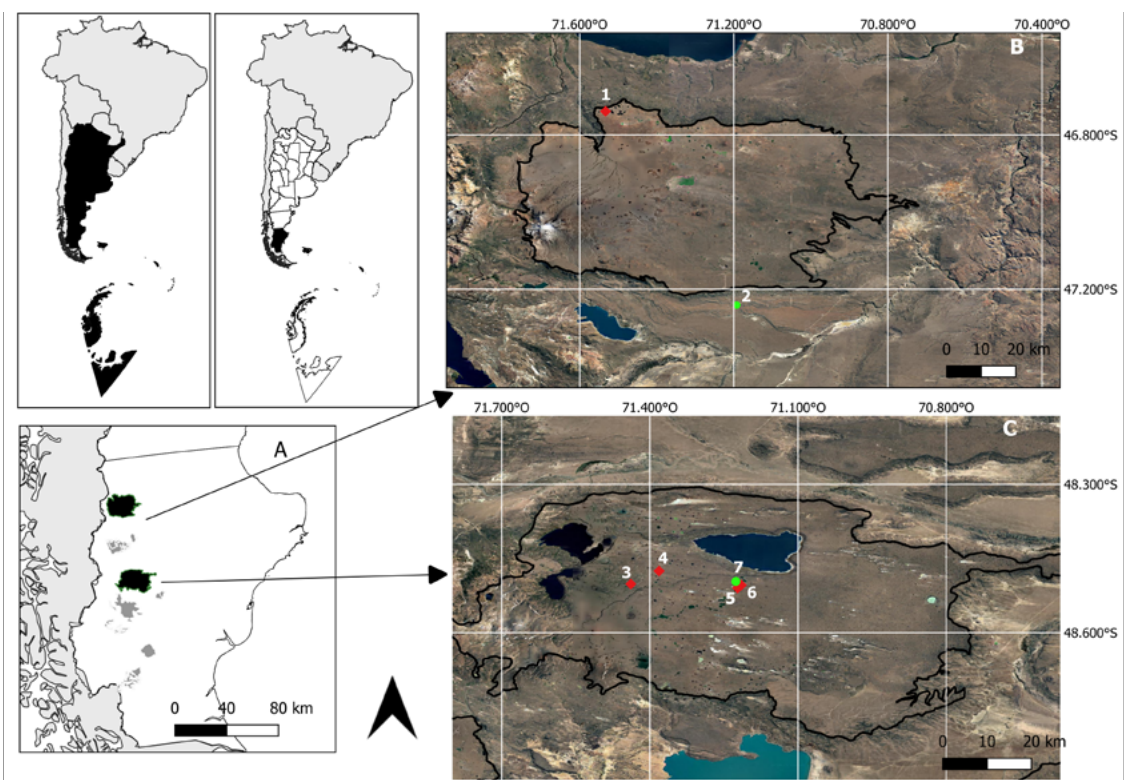


**Figure 1.** Study area in Santa Cruz Province, Argentina: A) Study area showing the important plateaus: in black, plateaus covered in this study; in grey, other important plateaus for the Hooded Grebe (*Podiceps gallardoi*). B) On Buenos Aires Lake Plateau, location of the lakes (red diamonds) where we collected eggs and *ex situ* breeding sites (green dots): 1 = LA4, 2 = Juan Mazar Barnett Biological Station. C) On Strobel Lake Plateau, location of the lakes (red diamonds) where we collected eggs and *ex situ* breeding sites (green dots): 3 = Rodríguez 19, 4 = Rodríguez 9, 5 = Nueve, 6 = Ocho, 7 = Laguna Verde.

(2016/2017) we tried two protocols simultaneously: A low temperature-high humidity (34.5-34.8°C/65-70%; $n$ = 7) and a middle temperature-high humidity (36.5-36.8°C/65-70%; $n$ = 4), but the chicks hatched immature and weak (i.e., the chicks hatched with their navels open, their back down incomplete, and their eyes closed). Then, due to the arid environment the Hooded Grebe inhabits, we wanted to try decreasing the humidity. So, also during the season 2016/2017, we used a low temperature-low humidity protocol (34.5-34.8°C/35-40%; $n$ = 4) with poor results. Finally, in the season 2017/2018, we tried a high temperature-low humidity protocol (37.1-37.5°C/35-40%; $n$ = 12). Because, subjectively, we obtained the strongest chicks in the first attempt, we decided to return to the high temperature-high humidity protocol in the 2019/2020 season ($n$ = 5). We had technical problems with the middle temperature-high humidity protocol. A hatcher (incubator at a lower temperature) broke, and the eggs suffered an abrupt drop in temperature (almost 2°C).

Daily, we weighed the eggs (scale accuracy 0.01g) to calculate the daily weight loss (Fig. 2C). We defined three intervals of egg-weight loss: interval 1 (0.6–0.9%), interval 2 (1.0–1.3%), and interval 3 (1.4–1.7%). Every three days, we candled the eggs to see embryo development. Over the last 2–3 days, once the eggs were internally pipped, we transferred them to a hatcher. The hatcher was always 0.5°C colder than the incubator in each protocol.

### Chick rearing

After hatching, each chick remained in the hatcher for two hours to dry its down before being moved to a breeding box (i.e., a container with a bottom heat source). This was at 36-37°C, like the temperature of a grebes back (Roesler 2016). Daily, the chicks were weighed (0.01 g), fed (Fig. 2D), and placed in a pool (Fig. 2E) to drink and defecate.

We created four day- and night-care scenarios, based on the interval between meals, and one without night feeding, applied according to the number of chicks obtained per season. The difference between treatments was in the frequency of nocturnal feeding. The chicks were fed every hour during the day (06:00-22:00 h) and every one, two, or four hours during the night (scenario one, two, and four hours, respectively). In addition, we used one treatment which did not include night feeding at all (scenario none). Since grebes need to be in the water to defecate and exercise (Gage & Duerr 2007), feeding was always accompanied by a swimming session. In the 'none scenario', the chicks passed through the pool once during the night to stimulate defecation following MacVean (1988). We also created the first scenarios following MacVean's work (1988). Then, the protocols were adapted according to the results or perceptions obtained across the

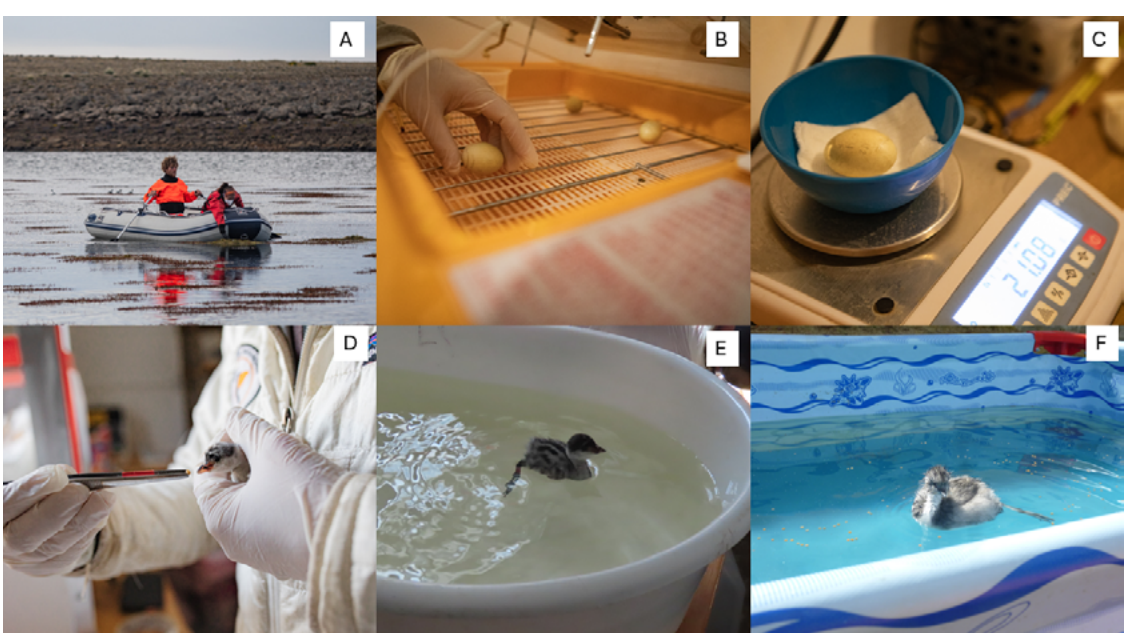


**Figure 2.** Working methodology used for Hooded Grebe (*Podiceps gallardoi*) and the Silvery Grebe (*P. occipitalis*): A) Egg collection, B) Incubation, C) Egg weighing, D) Hand feeding of chicks, E) Swimming session, F) Independent feeding of chicks in larger pools.

seasons. In the first two weeks, chicks were fed with tweezers. Then, chicks began to fish for live prey (amphipods) in the pool, which is consistent with their normal feeding behavior. During the first week, chicks were placed in water only long enough to stimulate defecation (15–30 s). After the first week, the time spent in water was gradually lengthened. Chicks were retired from the pool when they showed signs of stress (i.e., vocalizations, restlessness). After four weeks, the only chick alive spent all day in the water and was only retired from the pool at night. The pool was supplemented with live prey (amphipods) collected in the lakes. After seven weeks, following the first plumage transition, it was always in the pool. In the first week, we used a small plastic tub (40 cm x 25 cm x 10 cm). In the second week, we used a 70 cm x 40 cm x 20 cm plastic tub. After three weeks, we placed the chick in a larger pool (1.30 m x 0.95 m x 0.40 m, Fig. 2F). The water used to fill the pools came from local rivers through the ranches' canal system. As it is a gregarious species, we placed mirrors in the pool and breeding box to simulate the presence of other individuals. To define the minimum age of release, we considered it to be older than a month, as juveniles typically become independent of their parents at approximately that age (Roesler 2016). We also thought that it had completed the first plumage transition, which occurs between six and seven weeks of life. We used three food options applied according to the chicks obtained and the food available per season: hypoallergenic cat food and trout (2015/2016), amphipods collected in the lakes (2015/2016-2016/2017-2017/2018-2019/2020), and bloodworms rehydrated with water (2019/2020). We also offered feathers to all the nestlings (Storer 1961, Roesler 2016). We performed a necropsy on all the dead chicks to find out the cause of death.

### Data analysis

We considered the response variables hatching success (i.e., whether the egg hatched) and survival time (in hours) of the chicks up to 15 days of life (360 h) or until death. We consider survival through 15 days because, at this age, the chicks are less dependent on external care (e.g., they forage for food and stay longer in the water). To evaluate the effects of incubation stage at collection, transport duration, and incubation protocol on hatching success, we ran generalized linear models with a binomial distribution and a logit link function. We tested univariate models with the three predictor variables, as well as the interaction between natural incubation days and transfer time. For this analysis, we used only Hooded Grebe eggs. Model selection was performed using the corrected Akaike information criterion (AICc). Assumptions were checked using the *DHARMa* statistical package (Harting 2024). To compare daily weight loss between hatched and unhatched eggs, we performed a Mann-Whitney U test. We evaluated the effects of incubation protocol, daily egg weight loss, and chick care frequency on early chick survival time using Kaplan-Meier survival analysis and used the log-rank test for between-group comparisons. We compared the survival of chicks with night feeding versus those without night feeding using a Mann-Whitney U test. We considered chicks that received only one-night feeding within the group without night feeding because we think that four hours is a very long interval, as observed in lakes (Roesler 2016). All analyses were performed in R 4.1.0 (R Core Team 2021).

## RESULTS

We collected a total of 45 eggs in nine removal events, comprising 42 Hooded Grebe eggs and three Silvery Grebe eggs. One Hooded Grebe egg broke during measurement and was discarded. We did not detect unviable eggs by candle. Mean Hooded Grebe egg length was 4.58 ± 0.18 cm (range = 4.20–5.10 cm; $n$ = 41); mean Hooded Grebe egg width was 3.08 ± 0.07 cm (range = 2.90–3.20 cm; $n$ = 41). Mean Silvery Grebe egg length was 4.33 ± 0.32 cm (range = 4.10–4.70 cm; $n$ = 3); mean Silvery Grebe egg width was 2.90 ± 0.10 cm (range = 2.80–3.00 cm; $n$ = 3).

### Hatching success

Of the 44 eggs, seven (Hooded Grebe) were collected during the first incubation period (1-7 days), 17 (Hooded Grebe) were collected during the second incubation period (8-14 days), and 15 (12 Hooded Grebe / 3 Silvery Grebe) were collected during the third incubation period (15-21 days). Five eggs (Hooded Grebe) could not be classified because they did not hatch therefore, we could not backdate the laying day (no evidence from observations of the colony). Mean egg weight for Hooded Grebe for the first incubation period was 23.70 ± 1.80 g (range = 20.41–26.44 g; $n$ = 7), for the second incubation period, 21.98 ± 1.54 g (range = 18.87–24.42 g; $n$ = 17) and for the third incubation period, 21.40 ± 1.51 g (range = 19.24–24.37 g; $n$ = 12). Mean egg weight for Silvery Grebe, all of which were obtained in the third incubation period, was 18.26 ± 1.77 g (range = 17.00–20.28 g; $n$= 3). The hatching rate for all eggs was 73% (32/44) – 57% (4/7) for eggs collected in the

first incubation third, 82% (14/17) in the second, and 93% (14/15) in the third (Fig. 3).

We documented transport time ranging from 16 minutes to nine hours. To analyze the effect of the incubation protocol on hatching, we discarded the eggs incubated with the middle temperature-high humidity ($n$ = 4). The allocation of eggs among the other four protocols was as follows: seven eggs (low temperature-high humidity), four eggs (low temperature-low humidity), 17 eggs (high temperature-high humidity), and 12 eggs (high temperature-low humidity).

Using AICc for small sample sizes for model selection to assess the effect of variables on hatching success, the univariate model with the predictor variable of days of natural incubation at the time of collection (numerical) was selected as the best model (relative weight = 0.69, Table 1). However, no significant differences were detected (Z = 0.688, $p$ < 0.491).

Mean daily egg-weight loss during incubation was 1.05 ± 0.35 % (range = 0.31–1.61%; $n$ = 44). We did not detect significant differences in weight loss for hatched versus unhatched eggs (U = 266, df = 1, $p$ = 0.673).

### Survival in the initial stage

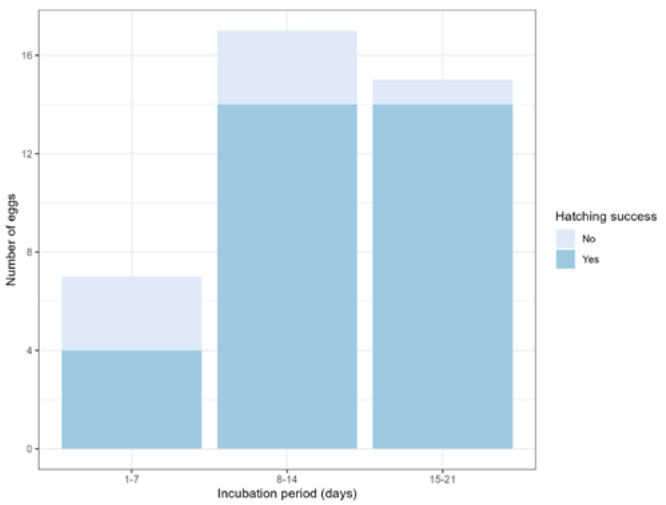


**Figure 3.** Hatching success of Hooded Grebe (*Podiceps gallardoi*) and Silvery Grebe (*P. occipitalis*) eggs as a function of the incubation period during which the egg was collected.

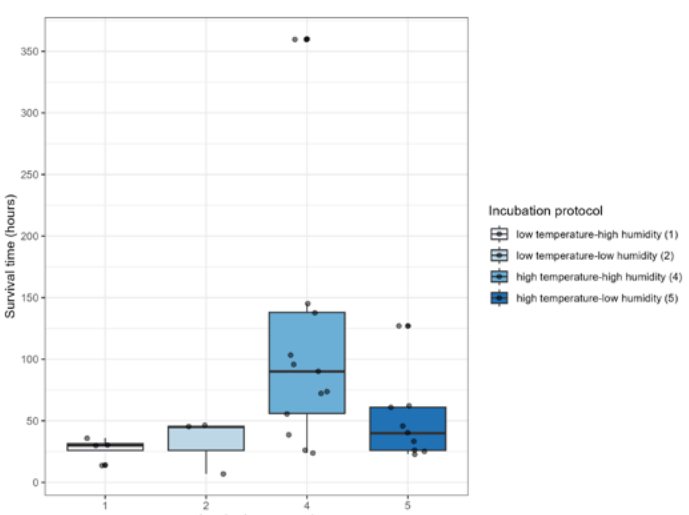


**Figure 4.** Graph made from raw data showing survival time of Hooded Grebe (*Podiceps gallardoi*) and Silvery Grebe (*P. occipitalis*) chicks according to the incubation protocol.

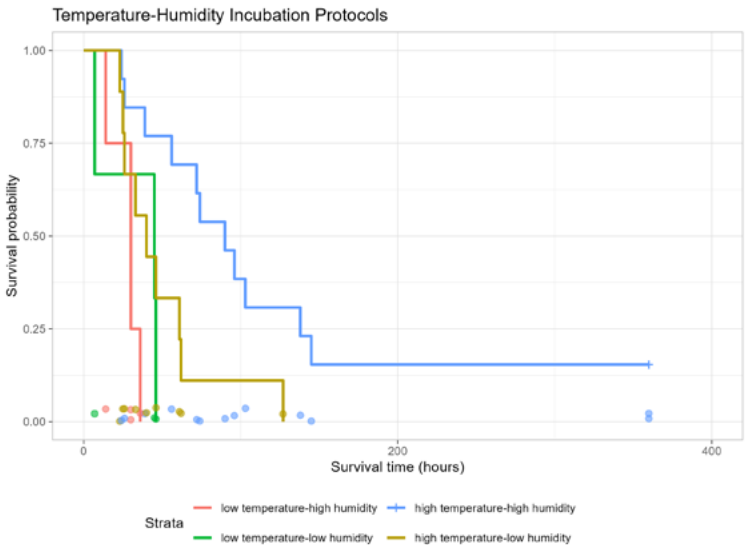


**Figure 5.** Kaplan-Meier survival curves comparing the survival probability of Hooded (*Podiceps gallardoi*) and Silvery (*P. occipitalis*) Grebes chicks hatched from eggs incubated with different temperature and humidity protocols. The censoring lines represent chicks that did not die before 15 days of age.

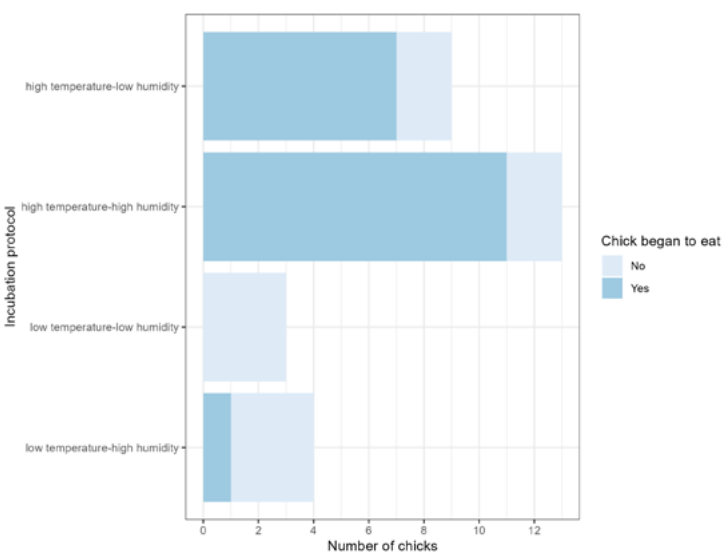


**Figure 6.** Proportion of Hooded Grebe (*Podiceps gallardoi*) and Silvery Grebe (*P. occipitalis*) chicks that never began to eat according to different temperature and humidity protocols.

**Table 1.** Multiple model selection analysis (AICc) values of the effect of incubation stage at collection time, transport duration, and incubation protocol on hatching success, including global and null models. Variables: Days_col: days of natural incubation at the time of collection, Transp_dur: duration of transport of eggs from the lakes to the rearing facilities, Incubation: incubation protocol.

| Intercep. | Days_col | Transp_dur | Incubation | Days_transp | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|---|---|
| 0.549 | 0.068 | | | | 2 | -19.081 | 42.5 | 0 | 0.689 |
| 3.636 | -0.177 | -0.008 | | 0.001 | 4 | -17.432 | 44.2 | 1.73 | 0.291 |
| 1.115 | | -0.002 | | | 2 | -23.295 | 50.9 | 8.42 | 0.010 |
| 0.882 | | | | | 1 | -24.786 | 51.7 | 9.16 | 0.007 |
| 0.288 | | | + | | 4 | -22.153 | 53.6 | 11.04 | 0.003 |

Thirty-two of 44 eggs hatched (i.e., 73%; 29 Hooded Grebe, 3 Silvery Grebe). The mean hatch weight for Hooded Grebe was 14.91 ± 0.85 g (range = 12.96–16.29 g; $n$ = 29) and 12.28 ± 1.40 g (range = 11.33–13.88 g; $n$ = 3) for Silvery Grebe. Mean survival time was 54.90 ± 35.94 h (range = 7.00–145.00 h; $n$ = 29) for Hooded Grebe and 274.33 ± 148.38 h (range = 103.00–360.00 h; $n$ = 3) for Silvery Grebe. Two Silvery Grebe individuals lived for more than 15 days; one died at day ~15 (362 h), and another was successfully released after 67 days (1608 h).

Mean survival time according to incubation protocol was 27.50 ± 9.43 h (range = 14.00–36.00 h; $n$ = 4) for the low temperature-high humidity protocol; 32.67 ± 22.23 h (range = 7.00–46.00 h; $n$ = 3) for the low temperature-low humidity protocol; 121.77 ± 112.18 h (range = 24.00–360.00 h; $n$ = 13) for high temperature-high humidity protocol; and 49.22 ± 32.64 h (range = 23.00–127.00 h; $n$ = 9) for the high temperature-low humidity protocol (Fig. 4). Kaplan-Meier survival analysis determined that there were statistically significant differences in survival between the different protocols ($\chi^2$ = 14.3, df = 3, $p$ = 0.003; Fig. 5). *Post hoc* comparisons using Bonferroni correction detected higher survival of chicks incubated with the high temperature-high humidity protocol compared to the low temperature-high humidity protocol ($\chi^2$ = 9.3, df = 1, $p$ = 0.013). Most chicks reared under the low temperature-high humidity (75%) and the low temperature-low humidity (100%) incubation protocols never began to eat, while only a few chicks in the high temperature-high humidity (15%) and high temperature-low humidity (22%) incubation protocols never began to eat (Fig. 6).

Mean survival time according to daily egg-weight loss was 35.70 ± 21.13 h (range = 07.00–84.00 h; $n$ = 10) for interval 1, 103.53 ± 110.26 h (range = 24.00–360.00 h; $n$ = 15) for interval 2 and 72.14 ± 39.16 h (range = 23.00–145.00 h; $n$ = 7) for interval 3 (Fig. 7). The Kaplan-Meier survival analysis determined that there were statistically significant differences in survival between groups ($\chi^2$ = 8.9, df = 2, $p$ = 0.012; Fig. 8). *Post hoc* comparisons using the Bonferroni correction detected a lower survival of chicks from group 1 compared to group 2 ($\chi^2$ = 6.5, df = 1, $p$ = 0.032).

Mean survival time according to chick care frequency was: 208.00 ± 214.96 h (range = 56.00–360.00 h; $n$ = 2) for scenario one h; 105.00 ± 43.95 h (range = 53.00–145.00 h; $n$ = 5) for scenario two h; 53.50 ± 20.49 h (range = 40.00–84.00 h; $n$ = 4) for scenario four h; and 89.73 ± 93.69 h (range = 23.00–360.00 h; $n$ = 11) for scenario none (Fig. 9). There were no significant differences in recorded survival times among the different night care scenarios (H = 3.76, df = 3, $p$ = 0.288). In the comparison between chicks with or without night feeding, mean survival time was 134.43 ± 107.31 h (range = 53.00–360.00 h; $n$ = 7) in the night feeding group and 80.07 ± 81.46 h (range = 23.00–360.00 h; $n$ = 15) in the group without night feeding. We did not detect significant differences in survival time between both groups ($p$ = 0.21).

After conducting necropsies, we suspect that most of the nestlings died from multiple organ failure due to compression damage caused by the 'bloat' (i.e., accumulation of gas in the stomach). One of the chicks had its stomach pierced by a feather, and one, which died at 362 hours, was due to gizzard impaction.

## DISCUSSION

Working on the conservation of endangered species often limits the number of case studies, making it impossible to develop balanced experimental designs. This makes it difficult to arrive at accurate statistical conclusions. However, the results of this work show clear trends that suggest the right direction to follow in the search for an *ex situ* breeding protocol for the Hooded Grebe.

Although we did not detect significant differences, we found that the hatching rate in eggs collected at advanced stages was notably higher than that of those gathered at early stages (93% vs. 57%). This agrees with the literature, which states that some bird species reared in captivity have a higher hatching success *ex situ* if they have a natural incubation period (MacVean 1988, Gage & Duerr 2007). This suggests that collecting eggs at a later stage of incubation would be preferable, but due to the low probability of success for some Hooded Grebe colonies (e.g., colonies exposed to strong windstorms, lakes with low water levels, and high evaporation rates), spending more time on the lake increases the probability of losing both eggs. For the time being, we have achieved the hatching success of eggs incubated in the wild for only five days. Finally, it's worth noting that our egg collections did not influence the reproductive success of any of the manipulated colonies (i.e., the parents raised one chick per nest).

An extremely valuable result for the future is that the transport method we used proved to be efficient. There were no differences in hatching success between longer and shorter duration trips, which increases the potential range of lakes from which to collect eggs.

During incubation, loss of about 10-20% of the egg's initial mass is essential for maintaining the egg's relative water content and forming the air cell (Ar & Rahn 1980, Davis et al. 1984). Eggs that lose too much or too little water have a decreased probability of hatching (Hoyt 1979, Davis et al. 1988) and can affect the viability of the chicks (Gage & Duerr 2007). We did not detect significant differences in mass losses between hatched and unhatched eggs; however, we observed that chicks hatched from eggs with daily mass losses below 1% had lower survival rates. This finding suggests that Hooded Grebe eggs could lose 21% or more of the initial mass.

An important variable for the proper development of the chicks is the incubation parameters (temperature and humidity), as they influence embryonic growth and the body condition of chicks (Barri 2008, DuRant et al. 2010). We did not find differences in hatching success between proposed incubation protocols with high and low temperatures and humidities. However, significant differences in chick survival were observed in relation to the incubation protocol. Chicks hatched using a high-temperature and high-humidity protocol had higher survival rates compared to those incubated at a low temperature and high humidity. Nevertheless, the most important thing to highlight is that none of the chicks that hatched from eggs incubated at low temperatures began to feed.

Although we did not obtain conclusive results, we observed a tendency for higher survival in chicks that were fed more frequently. Grebes are susceptible to the accumulation of gas in the stomach, usually called 'bloat', with the consequent compression of organs that leads to the death of the individual due to multiple organ failure (Gage & Duerr 2007). This ailment was the cause of death for the majority of chicks in this study. These results suggest the need for nearly constant feeding to maintain gastrointestinal motility (Barrett et al. 2010) and prevent gas accumulation (Gabarain 2021). This extraordinarily high and constant feeding rate is consistent with behavioral observations of individuals in the wild (Roesler 2016).

Nutritional requirements for grebes have not been established yet. As precocial birds, they need to be fed live prey, such as small insects, to stimulate foraging behavior (Padilla 2014). Hooded Grebe chick diet, estimated from the isotopic signature of two individuals found dead at a lake, is composed of a mixture of food items, 78% of which consists of chironomid larvae, and the remaining 22% was made up of a combination of amphipods, copepods, and *Daphnia* sp. (Lancelotti 2009). In addition, it has been observed that parents frequently give feathers to the chicks

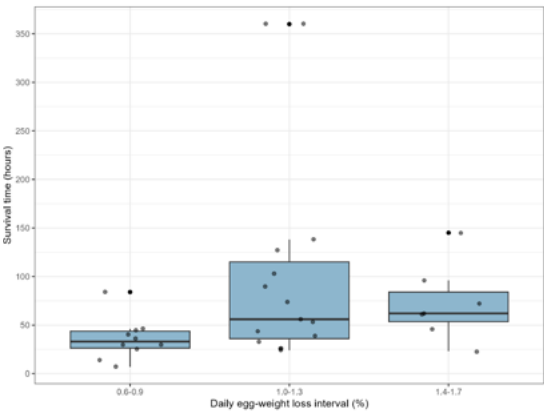


**Figure 7.** Graph made from raw data showing survival time of Hooded Grebe (*Podiceps gallardoi*) and Silvery Grebe (*P. occipitalis*) chicks according to the daily egg-weight loss interval.

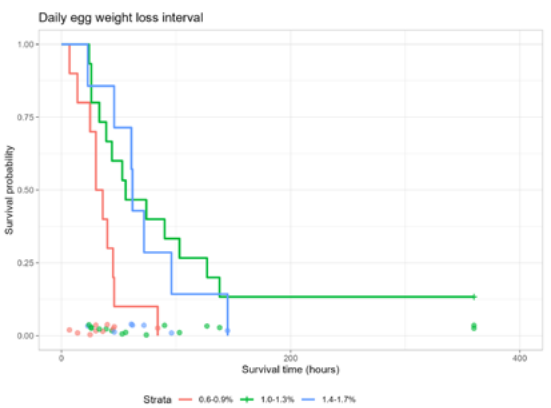


**Figure 8.** Kaplan-Meier survival curves comparing the survival probability of Hooded (*Podiceps gallardoi*) and Silvery (*P. occipitalis*) Grebes chicks hatched from eggs with different egg-weight loss. The censoring lines represent chicks that did not die before 15 days of age.

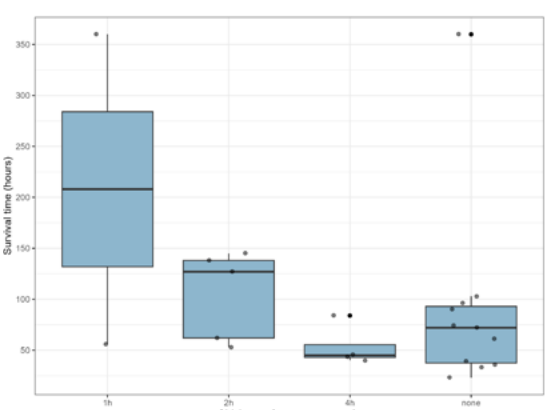


**Figure 9.** Graph made from raw data showing survival time of Hooded Grebe (*Podiceps gallardoi*) and Silvery Grebe (*P. occipitalis*) chicks according to the chick care frequency scenario.

soon after hatching (Roesler 2016), a behavior also observed in all the grebe species of the genus *Podiceps* (Fjeldså 2005). In this study, the administration of different foods was not standardized and was mainly based on the resources available in the lakes. For this reason, we excluded this variable from the analyses.

In summary, we describe the first *ex situ* hand rearing trials of Hooded and Silvery Grebe, where we successfully reared and released a single Silvery Grebe. At the time of release, the individual was already exhibiting natural behaviors typical of the species (i.e., fishing, diving, grooming). We released it into a lake used for fishing large trout, which ensures that it provides food for grebes. Additionally, this lake is often used by some grebes as a wintering site. On the release day, there were more than 700 Silvery Grebes in the lake. We marked the individual with an orange ring on the right leg, but unfortunately, we have not seen it again. The large number of Silvery Grebes on the plateaus makes locating and identifying specific individuals difficult. Currently, we are collaborating with universities and other partners on the development of a suitable transmitter for grebes. However, it is a challenging task the transmitter needs to weigh only a couple of grams, with a battery life prepared to support extended periods in cold, fresh, and saltwater, among other things.

Although the results are preliminary, mainly due to the low number of events analyzed, we observed tendencies in the different variables considered that could indicate how future experiments should be designed. It should be noted that when working with a species with a reduced population (less than 400 breeding pairs) and with extreme variability in reproductive attempts and success amongst seasons (seasons without colony formation), it is not possible to guarantee an adequate number of cases for carrying out sophisticated analyses (especially in terms of statistical treatment). It is also very ambitious to propose a static experimental design. It is valid to consider conducting some experimental tests with the Silvery Grebe, which can help refine procedures and methods. However, this may have its limitations due to the degree of specialization of the Hooded Grebe to the plateau environment; the information collected with the Silvery Grebe may not be directly applicable to the Hooded Grebe. Considering the critical situation of the Hooded Grebe, any conservation action requires extreme adaptability. Urgent need for results (in the short term) requires that the protocols be adapted not only based on statistically significant results but also on empirical information and even anecdotal data. This urgency makes it even more challenging to obtain large sample sizes. It would be extremely useful to have a quantity of data that would allow multifactorial analysis to evaluate how the different variables, currently analyzed independently, interact to affect both hatching success and chick survival. Understanding the effects of these interactions may help maximize the survival success of this imperiled species.

### Next steps and management

So far, we have learned how to retrieve eggs from nests and resolve the logistics of safely transporting them to breeding facilities, but it is important to determine the minimum natural incubation time required to proceed safely with artificial incubation, given the possibility of recovering all of the eggs from colonies at risk of destruction at any time from laying. We have made progress in the incubation process, resulting in the hatching of chicks with a reasonable degree of maturity (Gabarain 2021). However, the safe range of egg mass loss for the species is still to be determined, which is essential for the hatching of healthy chicks (Gage & Duerr 2007). The next step is to prevent the two leading causes of death in chicks: starvation and bloat. Chicks may require some form of early stimulation to encourage them to start eating. Additionally, more assiduous feeding (perhaps every 30 min) could prevent gas buildup by stimulating gastrointestinal motility. Finally, finding a highly digestible, balanced feed that reduces bloating and facilitates feeding logistics is essential.

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# OPTIMIZING THE USE OF GPS DEVICES TO ESTIMATE HOME RANGE AND FORAGING AREAS IN SEABIRDS: THE IMPERIAL SHAG AS A CASE STUDY

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**ABSTRACT:** Although GPS devices are widely used to delineate animal use areas, the sample size required to yield statistically robust estimates while minimizing animal welfare concerns is seldom assessed. In this study, we assessed how sample size (i.e., the number of individuals equipped with GPS devices) affects the accuracy of estimating both the total area of active use and the core foraging area of the Imperial Shag (*Leucocarbo atriceps*). We analyzed data from 140 breeding adults tracked over seven breeding seasons at Punta León (Chubut, Argentina). For each season, estimates of active use and core foraging areas were derived by progressively increasing the sample size from one to 20 individuals. Additionally, given sexual differences in foraging behavior, use and core foraging areas were estimated separately for females and males by progressively increasing sample sizes from one to 10 individuals per sex and year. On average, a minimum of 13 individuals was required to achieve < 5% increments in estimated area sizes. Tagging between 10 and 12 males and females was sufficient to estimate use and core foraging areas with an error below 5%. This study provides a straightforward approach to determine the minimum number of birds to tag, which can be adapted to other species with comparable movement patterns.

**KEYWORDS:** *birds, Global Positioning System, GPS, home range area, IBAs, sample size*

Animals perform a wide diversity of movements, both to acquire resources (i.e., food, mate, and shelter) and to escape from predators (Swingland & Greenwood 1983). These movements influence the configuration of population distribution patterns, the ecological role of species, and the spread of diseases, among other ecosystem characteristics (Nathan 2008, Kays et al. 2015). In this way, the analysis of animal movement has been central to studies in ecology, behavior, evolutionary biology, and environmental ecology (Nathan et al. 2022).

Among the most widely used electronic devices are Global Positioning Systems (GPS), which record positional information (latitude – longitude) at time intervals that may vary from seconds to days (Quintana et al. 2024). The information collected by these loggers allows, for example, the analyses of the trajectories of instrumented individuals and the determination of population use areas (Langley et al. 2021). In the field of conservation, positional data obtained through the use of GPS devices contribute to the design of management plans. These data allow the evaluation of the degree of overlap between the areas and routes used by individuals and various anthropogenic activities, such as commercial fishing (Copello & Quintana 2009, Yorio et al. 2010, Copello et al. 2014, 2016), the distribution and abundance of plastic pollutants (Blanco et al. 2022,

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Clark et al. 2023), and agriculture (Lenz et al. 2015), among others. In turn, information on movement and space use obtained from GPS devices is fundamental for the identification and delineation of Important Bird Areas (IBAs) and Key Biodiversity Areas (KBAs ; Eken et al. 2004, Beal et al. 2021).

In the particular case of birds, information obtained from the use of GPS devices plays a fundamental role in the program of BirdLife International to determine IBAs (Lascelles et al. 2016). This program aims to define key areas for conservation at global and regional levels (Thiollay 2002, Donald et al. 2019). Although IBAs were originally developed and applied in terrestrial and freshwater environments (Fishpool & Evans 2001), their application in marine environments has become widely practiced in recent decades (BirdLife International 2009). For their identification, design, and monitoring, the positional information in time and space of seabirds obtained through the use of GPS devices is fundamental (Lascelles et al. 2016, Beal et al. 2021).

A recent review of the use of biologgers in South American seabirds indicates that the use of GPS devices has encompassed 28 species belonging to nine families and five orders, and that almost all of the consulted publications (more than 250) contain information derived from positioning devices (Quintana et al. 2024). Despite their widespread use and the relevance of obtaining information that allows, for example, the proper delineation of IBAs and KBAs, studies analyzing the minimum number of animals to be tagged for the correct identification of the use areas of a given population are virtually nonexistent (Soanes et al. 2013, 2014, Lascelles et al. 2016, Beal et al. 2021, Shimada et al. 2021, He et al. 2023). In most cases, the number of equipped animals is mainly subject to the availability of time and funds for the acquisition and deployment of instruments. However, an insufficient sample size may compromise the robustness of population inference (Lindberg & Walker 2007, Hebblewhite & Haydon 2010, Soanes et al. 2013), whereas an excessive sample size may have ethical implications related to animal welfare (Bodey et al. 2018, Quintana et al. 2024, Arrondo & Pérez-García 2025). Thus, analyzing the optimal use of technology becomes important for the efficient allocation of funds and time invested in data collection and analysis, and for considering the ethical aspects related to animal welfare by avoiding excessive manipulation of individuals (Soanes et al. 2013, Williams et al. 2020, Quintana et al. 2024).

The goal of this study was to evaluate the effect of sample size (i.e., number of individuals tagged with GPS devices) on the precision of estimating the use of marine areas. As a case study, we used the Imperial Shag (*Leucocarbo atriceps*), a diving seabird with benthic habits (Malacalza et al. 1994, Quintana et al. 2011, Gómez Laich et al. 2012). We examined interannual variability in the minimum sample size (i.e., birds to be instrumented) required to determine the size of: a) active use marine areas (transit and feeding); and b) core foraging areas (where shags dive in search of prey). We carried out these estimations both for the population as a whole and separately for each sex, given the sexual dimorphism in size (Svagelj & Quintana 2007), as well as the differences in behavior and space use reported in previous studies (Quintana et al. 2011, Gómez Laich et al. 2012).

## METHODS

### Study species

The Imperial Shag is a diving seabird whose distribution along the Argentine coast extends from Punta León (43°S) in Chubut Province to the Beagle Channel (55°S) in Tierra del Fuego Province (Frere et al. 2005, Quintana et al. 2022). During the breeding season, these birds behave as central-place foragers (Orians & Pearson 1979), making regular feeding trips to the sea and returning to the colony to incubate the clutch and protect and feed the chicks (Quintana et al. 2011, 2022). Males and females exhibit sexual size dimorphism (Svagelj & Quintana 2007) and show spatial segregation in relation to foraging areas (Quintana et al. 2011) and differences in feeding and diving behavior (Gómez Laich et al. 2012).

### Database and study site

For this study we used a database of at-sea positions obtained from the deployment of GPS loggers during the foraging trips of breeding adult Imperial shags from the Punta León colony (43°04'S, 64°29'W), Chubut, Argentina (Fig. 1). Thus, we used a long-term dataset that includes information obtained from the instrumentation of a total of 140 individuals (20 individuals per year, 10 of each sex) over seven breeding seasons (2008–10, 2013, 2015–17). All instrumented shags were in the early chick-rearing period (four to 15 days old). To attach the devices, we removed the animals from their nests using a hook specially designed for this task and determined the sex of each individual from its vocalizations (males produce a '*honk*' and females a '*hiss*'; Malacalza & Hall 1988, Svagelj & Quintana 2007). We placed the GPS devices on the lower back using Tesa tape model 4621 (Wilson et al. 1997), and captured and instrumented each bird in approximately five minutes.

In no case did the weight of the device exceed 3% of the animal's body mass (Kenward 2001). During the seven years of study we used three types of loggers: (1) GPS (GPSlog, Earth and Ocean Technologies, Kiel, Germany, 95 × 48 × 24 mm and 65 g); (2) MiniGPS (Earth and Ocean Technologies, Kiel, Germany, 45 × 30 × 20 mm and 30.5 g); and (3) AXY-Trek (TechnoSmart, Rome, Italy, 40 × 20 × 8 mm and 25 g). In total, we instrumented 36 individuals with GPS devices (13 females, 23 males), 66 with MiniGPS devices (38 females, 28 males), and 38 with AXY-Treks (19 females, 19 males). In all cases, we programmed the instruments to record latitude and longitude at a frequency of 1 Hz (one datum per second), and they remained on the birds for a single feeding trip at sea. Upon return from the trip, we recaptured the birds in the same way described above, and the instruments and Tesa tape were carefully removed. We carried out this procedure in less than three minutes.

### Data analysis

#### Classification of positions

Following the methodology proposed by Quintana et al. (2011), we classified each of the positions recorded during feeding trips at sea according to the following behaviors: flight, floating, or diving. To do this, we used algorithms obtained from the observation of the frequency distribution of the horizontal travel speed associated with each position and the duration of interruptions in the GPS signals generated by the lack of transmission from the device when animals are underwater (Quintana et al. 2011). We classified as 'flight' all positions with speeds greater than 3 m/s, as 'diving' all positions with speeds equal to or less than 3 m/s and an interruption greater than or equal to 8 s, and as 'floating' positions with speeds equal to or less than 3 m/s and an interruption shorter than 8 s (Quintana et al. 2011).

#### Determination and calculation of marine areas of active use and core foraging areas

To calculate marine areas of active use and core foraging areas, we first constructed a grid with 1 km² cells in the marine zone surrounding the colony (Page et al. 2006). This grid was built using the POSGAR belt 3 projection (Alberdi & Erba 2022), which resulted in a total of 6768 cells. Thus, for each breeding season we calculated the size of the marine use area by counting the

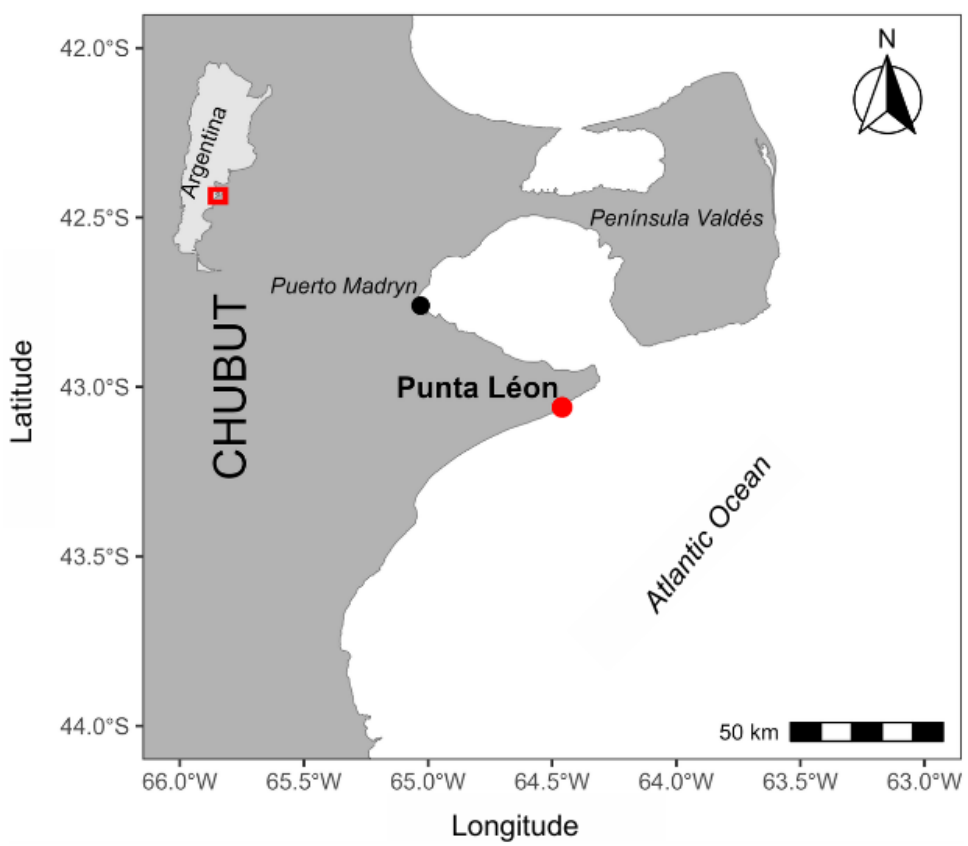


**Figure 1.** Location of the Imperial Shag (*Leucocarbo atriceps*) colony at Punta León on the coast of Chubut Province, Argentina.

total number of cells used by the animals considering all recorded positions (regardless of the behavior associated with each of them). For the determination of the core foraging area, in contrast, we counted the number of cells where animals performed dives (that is, only those positions classified as diving were used; Fig. 2).

For each season, we calculated the size of the active use and core foraging areas for an increasing sample of animals (from one to 20 individuals, representing all birds equipped per season). We selected the individuals included in each sample 20 times at random and with replacement. That is, for $n = 1$, we randomly selected with replacement one individual on 20 occasions and calculated the areas for each individual (20 active use areas and 20 core foraging areas in total). For $n = 2$, we randomly selected with replacement two individuals and calculated the areas for the 20 pairs of individuals, and so on. We used the same process to determine the minimum number of females and males to be tagged to establish both the size of the marine use area and the core foraging area for each sex. In this case, we calculated the areas for an increasing sample of individuals ranging from one to 10 according to the number of birds of each sex equipped in each season. We selected the individuals included in each sample 10 times at random and with replacement. Thus, for each sex we proceeded as follows: for $n = 1$, we randomly selected with replacement one individual 10 times and calculated the areas for each individual (10 active use areas and 10 core foraging areas in total). For $n = 2$, we randomly selected with replacement two individuals and calculated the areas for the 10 pairs of individuals, and so on. In this way, we obtained, for both females and males, 10 estimates of the active use area and 10 estimates of the core foraging area for each sample size (from one to 10).

Once the areas were calculated as a function of the increasing number of sampled individuals, we constructed accumulation curves of the size of the marine use area and core foraging area in relation to the number of individuals included in the sample, for the entire breeding population of the study site, composed of 13,200 individuals (6600 breeding pairs; Quintana et al. 2022). We fitted these curves using the Michaelis–Menten model with the function *drm* from the library *drc* (Knezevic et al. 2007) in the open-access software R version 4.2.3 (R Core Team 2022). The choice of this model was based on the fact

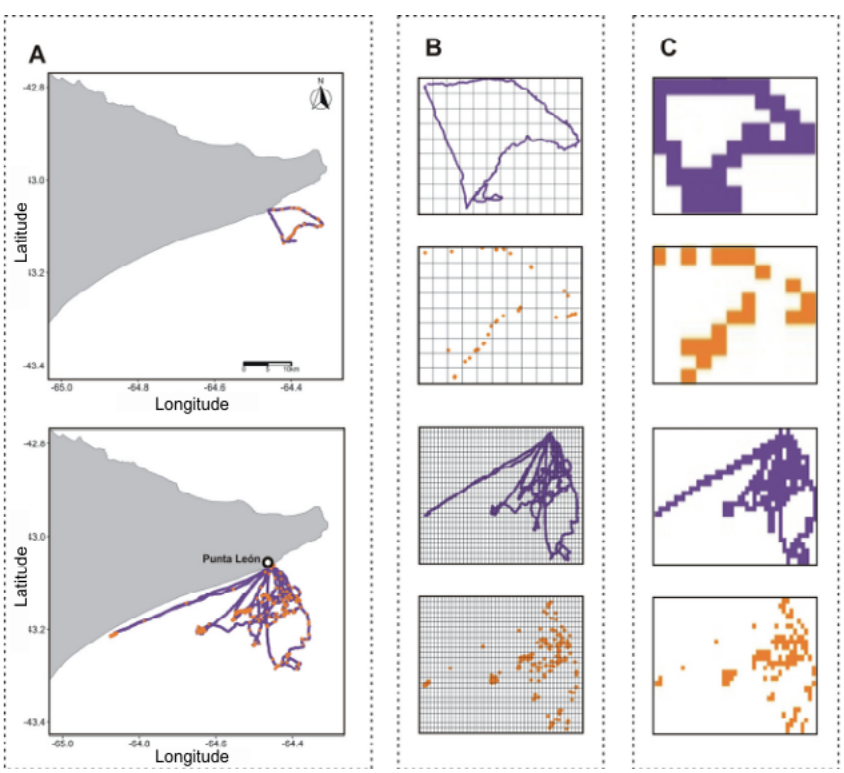


**Figure 2.** Determination of the marine areas of active use and core foraging of Imperial shags (*Leucocarbo atriceps*) equipped with GPS at the Punta León colony, Chubut, Argentina, during the chick-rearing period. A) Foraging trajectories of a single individual (upper panel) and of 20 individuals (lower panel) during one breeding season, B) overlay of the trajectories on a grid with 1 km² cells, and C) cells used during foraging trips. Purple points represent all recorded positions, while orange points show only those classified as dives.

that in several species of seabirds during the breeding season, the relationship between the number of individuals considered and the size of the active use and/or core foraging areas tends to stabilize as sample size increases, reaching an asymptote that represents the maximum area used (Soanes et al. 2013). This pattern reflects the spatial, energetic, and temporal constraints faced by central-place foragers (Orians & Pearson 1979). In the case of the Imperial Shag, these limitations are related both to morphological and physiological factors, mainly associated with the trade-offs involved in being both a diving and flying bird (Bishop & Butler 1995, Watanabe et al. 2011, Wilson et al. 2012, Gómez-Laich et al. 2013), and to aspects of its reproductive biology linked to biparental care and the need to return periodically to the colony to attend and feed the chicks (Schreiber & Burger 2001, Quintana et al. 2011, Harris et al. 2013).

The Michaelis–Menten model has two parameters: 1) $V_{max}$, which corresponds to the value of the asymptote (that is, in this case, the size of the area that remains constant despite an increase in sample size), which from now on will be referred to as $A_{max}$; and 2) $K_m$, which in this study corresponds to the number of animals to tag for which the active use or core foraging area (depending on the case) is half the value of the area represented by the asymptote, which from now on will be referred to as $T_m$ (Johnson & Goody 2011; Fig. 3). Because $T_m$ constitutes a purely arithmetic parameter derived from the model equation and does not have practical significance for the objectives of this study, the results mainly discuss aspects associated with the parameter $A_{max}$.

### Statistical analyses

#### Determination of the minimum sample size

To analyze interannual variation in sample size (i.e., minimum number of individuals to be tagged) to estimate the size of the active marine use and core foraging areas of the entire population and for each sex, we determined the relevance of including the explanatory variable year in the Michaelis–Menten models and its effect on the parameters $A_{max}$ and $T_m$. To analyze the relationship between sample size and the size of active use and core foraging areas, we compared the following four models: 1) a model without including the variable year/sex as an explanatory variable, 2) a model including the effect of the variable year/sex on the parameters $A_{max}$ and $T_m$, 3) a model including the effect of the variable year/sex only on the parameter $A_{max}$, and 4) a model including the effect of the variable year/sex only on the parameter $T_m$. The four models were constructed using the function *nls* from the library *nlme* (Pinheiro et al. 2007). We ranked the models according to the minimization of the corrected AIC (AICc), subsequently calculated the ΔAICc between them, and selected the model with the lowest ΔAICc (Anderson & Burnham 2002). In those cases in which several models had a ΔAICc ≤ 4, we selected the most parsimonious model (i.e., the one that included fewer parameters; Lehikoinen et al. 2021). To calculate both the AICc and the AICc weight (AICcw) of each model, as well as the ΔAICc between models, we used the function *aictab* from the library *AICcmodavg* (Mazerolle 2020).

In all cases, we verified the assumptions of normality and homoscedasticity of the best model. If heteroscedasticity were detected, we modeled the variance using the variance structure *varExp*. In those cases in which the best-fitting model included the variable year, we performed contrast tests of the parameter $A_{max}$, $T_m$, or both (as appropriate) among all years through post hoc multiple comparison tests using the function *paircomp* from the library *aomisc* (Onofri 2020) with the Holm correction (Aickin & Gensler 1996). We estimated the increase in the size of the active use area and the core foraging area as a function of the number of shags included in the sample using the best-fitting model for each case. Subsequently, in order to evaluate with different levels of precision the size of the use and feeding areas by year/sex, we calculated the minimum sample size and its range from which adding one more individual to the sample resulted in an increase in area (active use or core foraging) of less than 5, 3, and 1%, with the 1% criterion representing the highest precision and the 5% criterion the lowest. To obtain the minimum and maximum values, that is, the range of the minimum sample size, we first calculated the confidence interval of the parameters of the best model for the active use marine area. Analogously, we obtained the confidence interval for the core foraging area. In both cases, the intervals were obtained using the function *confint* (Ripley et al. 2013). With the minimum and maximum values of each parameter we constructed the lower and upper curves of the relationship between area size and sample size. We used the lower curve to estimate the minimum value of the range of sample size from which the increase in area was less than 5, 3, and 1%, while we used the upper curve to estimate the maximum value (Fig. 3). We based the evaluation of differences in the sample size required to estimate the size of the marine active use area and core foraging area of individuals between years and between sexes

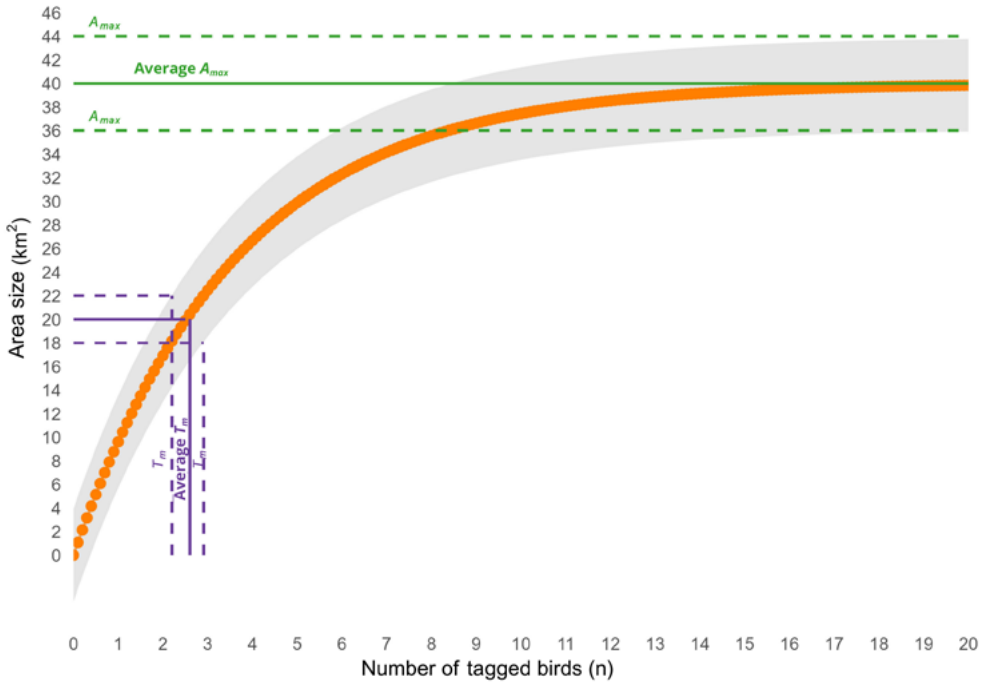


**Figure 3.** Illustrative example of the Michaelis–Menten model with its two parameters, $A_{max}$ and $T_m$. In orange, the relationship between area size and sample size (i.e., number of tagged birds) is shown, while the gray shading indicates the confidence interval of the curve. The parameters obtained from the model ($T_m$ = 2.5 and $A_{max}$ = 40) and the lower ($T_m$ = 3 and $A_{max}$ = 36) and upper ($T_m$ = 2 and $A_{max}$ = 44) values of each parameter obtained from the confidence intervals are also indicated.

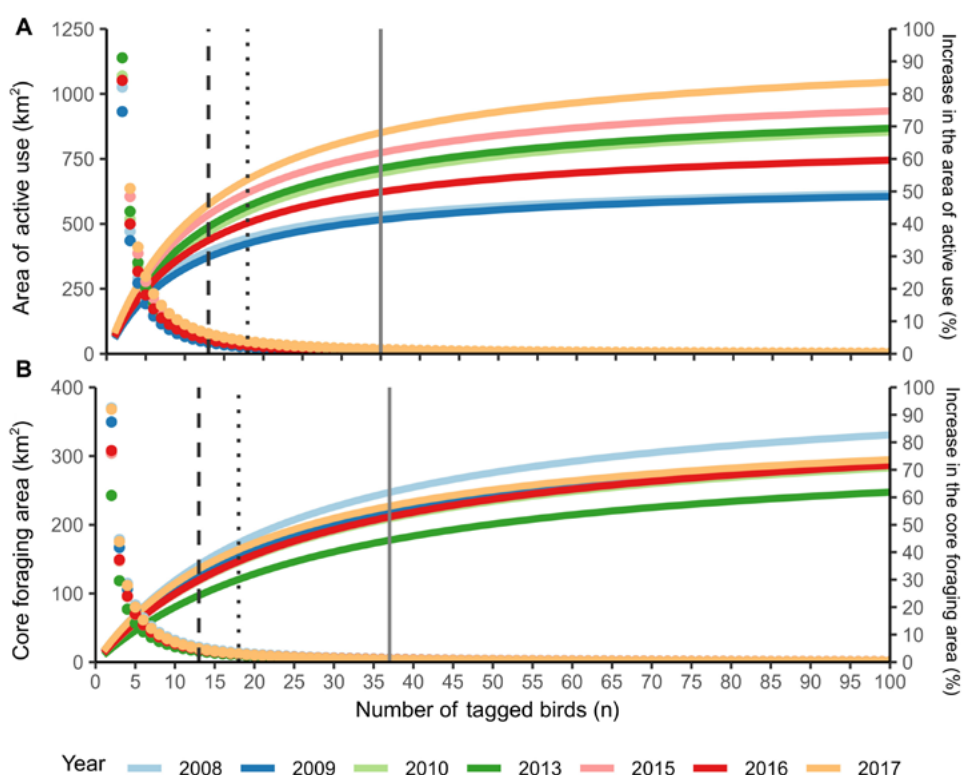


**Figure 4.** Sizes of the areas of active use (A) and core foraging (B) (solid lines) with their respective percentages of increase (dotted lines), in relation to sample size for the Imperial Shag (*Leucocarbo atriceps*), for the seven study years. In both graphs, the vertical dashed, dotted, and solid lines indicate the average minimum number of animals to instrument such that adding one more individual to the sample increases the area by less than 5%, 3%, and 1%, respectively.

within each year on the overlap of the ranges of predicted values for each case. We conducted all analyses with the open-access software R version 4.2.3 (R Core Team 2022) considering a significance level of 0.05.

## RESULTS

### Determination of the minimum sample size for the population

For all study years, the size of the active use area increased as the number of birds included in the sample increased until reaching an asymptote, and the relationship between both variables differed among years (Fig. 4A, Tables 1 & 2). The size of the active use area of the breeding population averaged 916 km² and ranged between 672 and 1169 km² (Table 2). The main differences in the sizes of the use areas corresponded to the 2008, 2009, and 2017 seasons. During the 2008 and 2009 seasons, the estimated areas used by breeding adults were smaller than in the other seasons (*post hoc* contrasts for parameter $A_{max}$ between 2008 and 2009 vs. 2010, 2013, 2015, 2016, and 2017; $p < 0.001$, Table 2), whereas during 2017 it was larger than in the other seasons (*post hoc* contrasts for parameter $A_{max}$ between 2017 and 2008, 2009, 2010, 2013, 2015, and 2016; $p < 0.050$, Table 2).

The model that best represented (i.e., best fit and parsimony) the relationship between core foraging area size and sample size included the explanatory variable year affecting parameter $T_m$ but not $A_{max}$. Thus, the size of the core foraging area of the breeding population did not differ among years and averaged 351 km² (Fig. 4B, Tables 1 & 2).

The average minimum number of animals to be tagged to estimate the size of the use area was 13 (range = 11–16), 18 (range = 15–22), and 35 (range = 27–42) for increases in area smaller than 5, 3, and 1%, respectively (Fig. 5A). In 2008 and 2009, the number of animals to tag was, in all cases, lower than in the other years, whereas in 2017 it was higher (Fig. 5A).

The size of the core foraging area of the breeding population (mean: 351 km²; range: 311–399 km²) did not differ among seasons (Table 2). In general terms, the average minimum number of shags to be tagged to estimate the core foraging area of the entire population showed less variation among years compared with the sample size required for the use area (Fig. 5B). The average minimum number of animals to be tagged to determine the core foraging area was 13 (range = 12–14), 19 (range = 17–19), and 39 (range = 37–40) with precisions smaller than 5, 3, and 1%, respectively (Fig. 5B). The main differences corresponded to the 2013 season, in which the sample size from which the increase in area was smaller than 5% was lower than in the other seasons (Fig. 5B). Likewise, the number of animals to be tagged from which the increase in core foraging area was smaller than 3% was lower in 2013 compared with 2008, 2009, and 2017, whereas the sample size for precisions smaller than 1% was similar across the seven study years, showing differences only between 2013 and 2008 (Fig. 5B).

### Determination of the minimum sample size for each sex

In all seasons, the size of the active use and core foraging areas for both females and males increased with increasing sample size until reaching an asymptotic value (Fig. 6). The effect of sex on the relationship between use area size and sample size varied among seasons (Table 3). Whereas in the 2008, 2010, 2013, and 2015 seasons no differences between sexes were observed (Fig. 6, Table 4), in 2009 and 2016 the use areas were larger for females and in 2017 for males (Fig. 6, Tables 3 & 4). During the study period, females and males showed the same average active use area size (parameters $A_{max}$), on the order of 600 km² (Fig. 6, Table 3). In general terms, the average number of animals to be tagged from which the increase in use area was smaller than 5, 3, and 1% was similar between sexes (Fig. 7A). Thus, the average minimum number of females to be tagged was 10 (range = 9–11), 14 (range = 12–15), and 25 (range = 22–28), and for males 10 (range = 8–12), 13 (range = 11–15), and 25 (range = 20–28), for area increases of 5, 3, and 1%, respectively (Fig. 7A). The largest difference between sexes in the number of birds tagged to estimate the use area occurred in 2009. In that season, more females than males were required to estimate the size of the use area (Fig. 7A).

The effect of sex on the relationship between core foraging area size and sample size also varied among seasons (Table 5). Whereas in the 2008, 2010, 2015, and 2016 seasons females and males showed feeding areas of similar size, during 2009, 2013, and 2017 females foraged over larger areas (Fig. 6, Tables 5 & 6). In general terms, during the study period females and males fed in areas of similar average size (parameters $A_{max}$), covering approximately 200–230 km² (Fig. 6, Table 6). Broadly speaking, the average number of animals to be tagged from which the increase in feeding area was smaller than 5, 3, and 1% was similar between sexes (Fig. 7B). Thus, the average minimum number of females to be tagged was 12 (range = 11–13), 17 (range = 14–19), and 32 (range = 26–36), and for males 12 (range = 10–14), 16 (range = 14–19),

**Table 1.** Michaelis–Menten models for the relationship between active use and core foraging area sizes as a function of sample size for the Imperial Shag (*Leucocarbo atriceps*). In each case, the best model is shown in bold. The table presents: the number of parameters (k), the difference in AICc between each model and the best-fitting model (ΔAICc), the AIC weights (AICcw), and the cumulative sum of AICcw weights (Cum.wt).

| Response variable | Model | k | AICc | ΔAICc | AICcw | Cum.wt |
|---|---|---|---|---|---|---|
| Active use area | **$A_{max}$~Year, $T_m$~ Year** | **15** | **30855** | **0.0** | **1.0** | **1.0** |
| | $A_{max}$~ Year, $T_m$~1 | 9 | 30871 | 16.2 | 0.0 | 1.0 |
| | $A_{max}$~1, $T_m$~ Year | 9 | 31029 | 174.4 | 0.0 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 32761 | 1906.3 | 0.0 | 1.0 |
| Core foraging area | $A_{max}$~ Year, $T_m$~ Year | 15 | 23414 | 0.0 | 0.5 | 0.5 |
| | **$A_{max}$~1, $T_m$~ Year** | **9** | **23415** | **0.6** | **0.4** | **0.9** |
| | $A_{max}$~ Year , $T_m$~1 | 9 | 23418 | 4.5 | 0.1 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 24655 | 1241.3 | 0.0 | 1.0 |

**Table 2.** Year-specific parameter estimates of the Michaelis–Menten model used to predict the sizes of active use and core foraging marine areas as a function of sample size for the Imperial Shag (*Leucocarbo atriceps*) at the Punta León (Chubut, Argentina) colony. Confidence intervals are indicated [Min–Max]. Significant multiple comparison tests for the parameter $A_{max}$ are indicated with an asterisk (*), whereas significant differences among years for the parameter $T_m$ are indicated with a black triangle (▵).
Active use area: * (2008 vs 2010, 2013, 2015, 2016, 2017); ** (2009 vs 2010, 2013, 2015, 2016, 2017); *** (2016 vs 2010, 2013, 2015, 2017); **** (2017 vs 2010, 2013, 2015); ▵ (2008 vs 2010, 2013, 2015, 2017); ▵▵ (2009 vs 2010, 2017).
Core foraging area: ▵ (2008 vs 2009, 2010, 2013, 2015, 2016, 2017); ▵▵ (2009 vs 2010, 2013, 2015, 2016, 2017); ▵▵▵ (2013 vs 2010, 2015, 2016, 2017); ▵▵▵▵ (2017 vs 2010, 2015, 2016).

| Year | $A_{max}$ | | $T_m$ | |
|---|---|---|---|---|
| | **Active use area (km²)** | **Core foraging Area (km²)** | **Active use area (*n* of animals)** | **Core foraging area (*n* of animals)** |
| 2008 | 674 [640-707] * | 399 [361-437] | 9 [8-10] ▵ | 24 [20-27] ▵ |
| 2009 | 672 [625-719] ** | 323 [293-352] | 10 [9-12] ▵▵ | 19 [16-22] ▵▵ |
| 2010 | 1010 [925-1095] | 364 [318-411] | 15 [13-17] | 27 [22-32] |
| 2013 | 1000 [920-1079] | 311 [267-355] | 14 [12-16] | 29 [23-35] ▵▵▵ |
| 2015 | 1066 [999-1133] | 356 [311-401] | 13 [11-14] | 26 [21-31] |
| 2016 | 819 [769-869] *** | 359 [311-407] | 11 [10-13] | 26 [21-31] |
| 2017 | 1169 [1072-1266] **** | 347 [313-382] | 13 [11-16] | 20 [17-24] ▵▵▵▵ |
| Mean | 916 [672-1169] | 351 [311-399] | 12 [9-15] | 24 [19-29] |

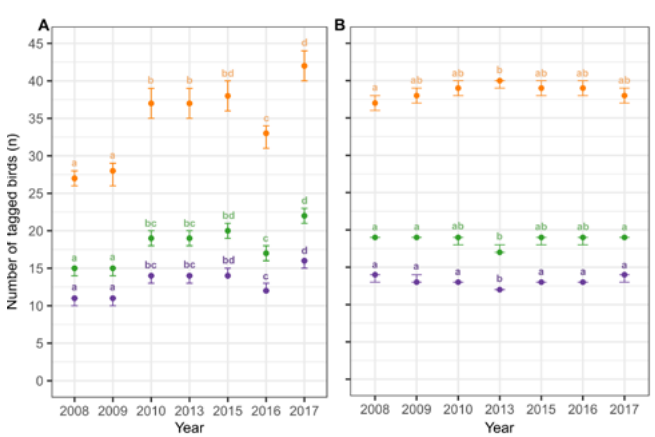


**Figure 5.** Number of Imperial shags (*Leucocarbo atriceps*) from the Punta León (Chubut, Argentina) colony tagged to estimate the size of the marine area of active use (A) and core foraging (B). Mean values and their ranges are presented for the sample size required so that the inclusion of one additional individual increases the estimated area by less than 1% (orange), 3% (green), and 5% (purple). Identical letters indicate no differences among years.

and 32 (range = 27–35), for area increases of 5, 3, and 1%, respectively (Fig. 7B).

## DISCUSSION

In this study, the long-term analysis (i.e., seven years) of interannual and sex-related variability in the active use and core foraging areas of the Imperial Shag allowed us to estimate the minimum number of individuals to be tagged to determine the sizes of these areas with three different levels of precision. To achieve this, we used a simple procedure that could potentially be applied to other species with similar ecological characteristics.

The sizes of core foraging areas were more consistent among seasons than that of active use areas, which resulted in lower interannual variability in the sample sizes required to estimate them. This consistency was even more evident when comparing between sexes. Long-term spatial stability in the use of foraging areas by shags from Punta León has previously been reported by Quintana et al. (2022) in a study spanning more than 10 years, and has also been documented in other seabird species when food patches remain relatively stable in time and space (Weimerskirch 2007, Rebstock et al. 2022, Regan et al. 2024). In our case, this stability is mainly related to the benthic feeding habits and the type of prey consumed by the Imperial Shag during the early chick-rearing stage (Harris et al. 2014, Quintana et al. 2022). During this period, adults obtain both their own food and that supplied to chicks primarily by capturing benthic prey such as notothenids (*Riberoclinus* sp.) and Raneya (*Raneya brasiliensis*; Malacalza et al. 1994, Ibarra et al. 2022). In general, benthic prey have a more restricted movement range than pelagic prey, making them a food source with greater spatiotemporal predictability (Elliott et al. 2009). In this context, it is reasonable to expect that the minimum number of Imperial shags to be tagged to determine foraging areas would be more consistent among seasons than the number required to determine active use areas. The latter are subject to intrinsic

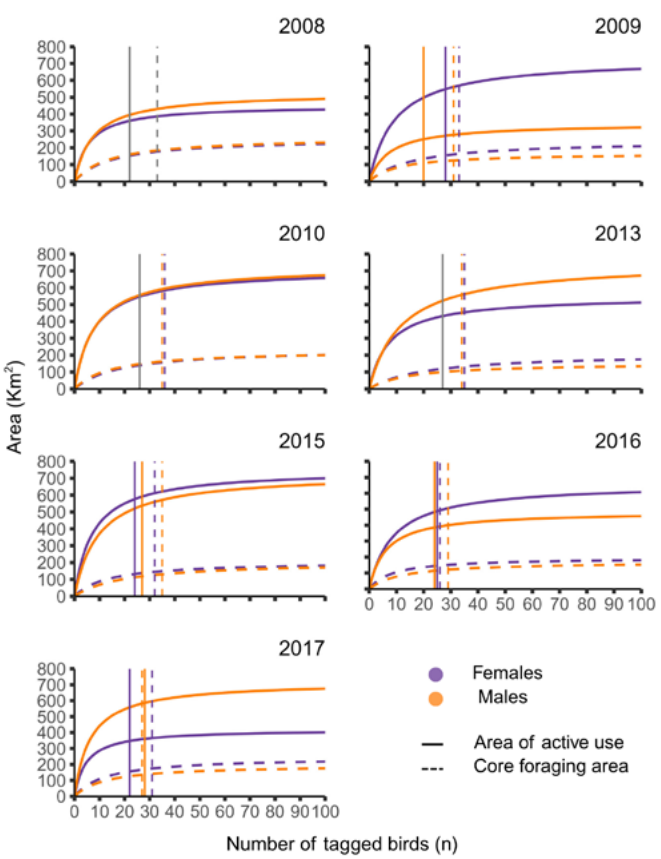


**Figure 6.** Sizes of the areas of active use (solid lines) and core foraging (dotted lines) of female and male Imperial shags (*Leucocarbo atriceps*) as a function of sample size, for the seven study years. Vertical lines (purple for females, orange for males, and gray if there were no differences between sexes) indicate the average minimum number of animals that must be tagged, from which point the inclusion of a new animal results in an increase of less than 1% in the size of the area of use (solid lines) or foraging (dotted lines).

**Table 3.** Michaelis–Menten models for the relationship between active use area size and sample size for female and male Imperial shags (*Leucocarbo atriceps*) across the seven study years. In each case, the best model is shown in bold. The table presents: the number of parameters (k), the difference in AICc between each model and the best-fitting model (ΔAICc), the AIC weights (AICcw), and the cumulative sum of AICcw weights (Cum.wt).

| Year | Model | k | AICc | ΔAICc | AICcw | Cum.wt |
|---|---|---|---|---|---|---|
| 2008 | **$A_{max}$~1, $T_m$~1** | **3** | **2090** | **0.0** | **0.5** | **0.5** |
| | $A_{max}$~Sex, $T_m$~1 | 4 | 2092 | 1.6 | 0.2 | 0.7 |
| | $A_{max}$~1, $T_m$~Sex | 4 | 2092 | 1.8 | 0.2 | 0.9 |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 2093 | 2.9 | 0.1 | 1.0 |
| 2009 | **$A_{max}$~Sex, $T_m$~1** | **4** | **2085** | **0.0** | **0.7** | **0.7** |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 2087 | 1.6 | 0.3 | 1.0 |
| | $A_{max}$~1, $T_m$~Sex | 4 | 2094 | 8.5 | 0.0 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 2308 | 223.2 | 0.0 | 1.0 |
| 2010 | **$A_{max}$~1, $T_m$~1** | **3** | **2214** | **0.0** | **0.6** | **0.6** |
| | $A_{max}$~Sex, $T_m$~1 | 4 | 2216 | 2.1 | 0.2 | 0.7 |
| | $A_{max}$~1, $T_m$~Sex | 4 | 2216 | 2.1 | 0.2 | 0.9 |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 2218 | 4.2 | 0.1 | 1.0 |
| 2013 | $A_{max}$~Sex, $T_m$~Sex | 5 | 2051 | 0.0 | 0.4 | 0.4 |
| | $A_{max}$~Sex, $T_m$~1 | 4 | 2052 | 1.0 | 0.3 | 0.7 |
| | $A_{max}$~1, $T_m$~Sex | 4 | 2053 | 2.0 | 0.2 | 0.9 |
| | **$A_{max}$~1, $T_m$~1** | **3** | **2053** | **2.2** | **0.1** | **1.0** |
| 2015 | **$A_{max}$~1, $T_m$~Sex** | **4** | **2121** | **0.0** | **0.5** | **0.5** |
| | $A_{max}$~Sex, $T_m$~1 | 4 | 2123 | 1.1 | 0.3 | 0.8 |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 2124 | 2.1 | 0.2 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 2174 | 52.3 | 0.0 | 1.0 |
| 2016 | $A_{max}$~Sex, $T_m$~Sex | 5 | 2053 | 0.0 | 0.5 | 0.5 |
| | **$A_{max}$~Sex, $T_m$~1** | **4** | **2053** | **0.2** | **0.4** | **0.9** |
| | $A_{max}$~1, $T_m$~Sex | 4 | 2056 | 3.5 | 0.1 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 2074 | 20.8 | 0.0 | 1.0 |
| 2017 | **$A_{max}$~Sex, $T_m$~1** | **4** | **2173** | **0.0** | **0.6** | **0.6** |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 2174 | 1.0 | 0.4 | 1.0 |
| | $A_{max}$~1, $T_m$~Sex | 4 | 2184 | 11.8 | 0.0 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 2309 | 136.5 | 0.0 | 1.0 |

conditions of individuals such as flight capacity and/or strategies required to reach feeding areas under changing climatic conditions (i.e., wind speed and direction, visibility, etc.).

In general terms, for each year, the minimum sample size required to estimate the core foraging area was larger than that required for the active use area. This suggests that variability among individuals is greater in feeding zones than in transit zones. One possible explanation is that shags share transit routes from the colony to food patches, using similar environmental cues and/or acquiring information through the observation of conspecifics (Ward & Zahavi 1973, Weimerskirch et al. 2010, Regan et al. 2024). However, once in foraging areas, individuals tend to disperse, which would reduce intraspecific competition for food (Davoren et al. 2003). This pattern is consistent with

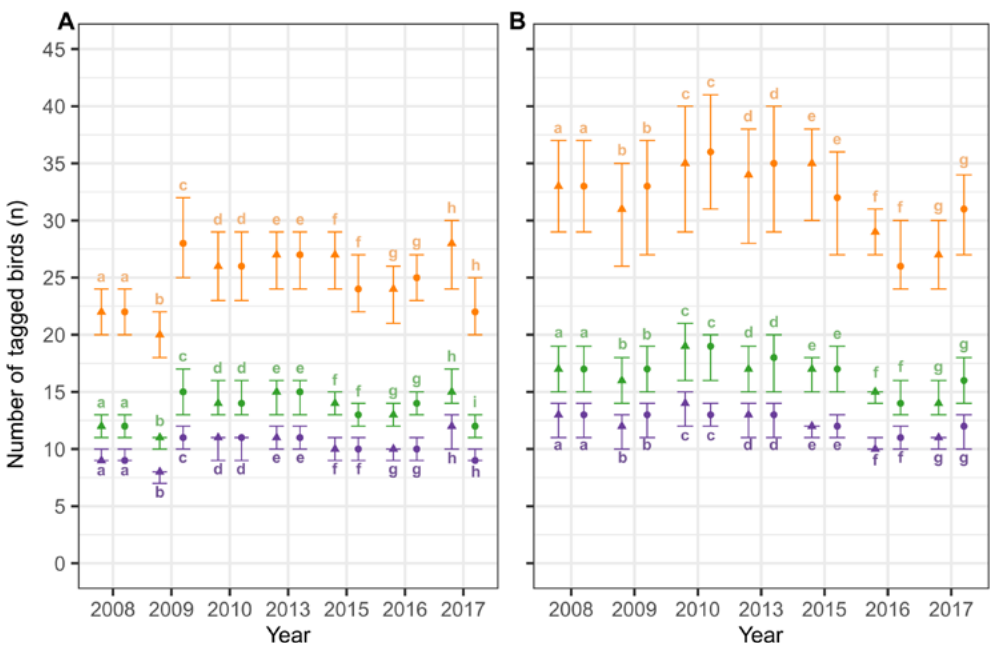


**Figure 7.** Numbers of female (circles) and male (triangles) Imperial shags (*Leucocarbo atriceps*) from the Punta León (Chubut, Argentina) colony tagged to estimate the size of the marine area of use (A) and foraging (B). Mean values and their corresponding ranges are presented for the sample size required so that the inclusion of one additional individual increases the estimated area by less than 1% (orange), 3% (green), and 5% (purple). Identical letters within each year for each percentage indicate no differences between sexes.

**Table 4.** Estimated parameters of the Michaelis–Menten model that showed the best fit for each year to predict marine area use as a function of sample size for female and male Imperial shags (*Leucocarbo atriceps*) at the Punta León (Chubut, Argentina) colony. The confidence interval [Min–Max] is indicated. Significant comparisons between sexes for the parameters $A_{max}$ and $T_m$ are shown in bold.

| Year | $A_{max}$ | | $T_m$ | |
|---|---|---|---|---|
| | **Female active use area (km²)** | **Male active use area (km²)** | **Female active use area (*n* of animals)** | **Male active use area (*n* of animals)** |
| 2008 | 452 [351-552] | 526 [425-627] | 6 [3-8] | 7 [5-10] |
| 2009 | **731 [547-914]** | **343 [270-417]** | 9 [5-13] | 7 [4-10] |
| 2010 | 709 [567-850] | 728 [534-922] | 8 [5- 10] | 8 [4-12] |
| 2013 | 550 [454-645] | 750 [545-956] | 7 [5-10] | 12 [7-17] |
| 2015 | 752 [638-865] | 729 [535-922] | **7 [5-9]** | **10 [5-14]** |
| 2016 | **661 [526-797]** | **484 [405-564]** | 9 [6-12] | 6 [4-8] |
| 2017 | **420 [338-503]** | **717 [601- 834]** | 5 [3-7] | 6 [4-8] |
| Mean | 610 [420-752] | 611 [343-750] | 7 [5-9] | 8 [6-12] |

**Table 5.** Michaelis–Menten models for the relationship between core foraging area size and sample size for female and male Imperial shags (*Leucocarbo atriceps*) for the seven study years. In each case, the best model is shown in bold. The table shows: the number of parameters (k), the difference in AICc between each model and the best-fitting model (ΔAICc), the AIC weights (AICcw), and the cumulative sum of the AICcw weights (Cum.wt).

| Year | Model | k | AICc | ΔAICc | AICcw | Cum.wt |
|---|---|---|---|---|---|---|
| 2008 | $A_{max}$~Sex, $T_m$~1 | 4 | 1623 | 0.0 | 0.4 | 0.4 |
| | $A_{max}$~1, $T_m$~Sex | 4 | 1623 | 0.0 | 0.4 | 0.7 |
| | **$A_{max}$~1, $T_m$~1** | **3** | **1624** | **1.5** | **0.2** | **0.9** |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 1625 | 2.1 | 0.1 | 1.0 |
| 2009 | **$A_{max}$~Sex, $T_m$~1** | **4** | **1583** | **0.0** | **0.5** | **0.5** |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 1584 | 0.8 | 0.3 | 0.8 |
| | $A_{max}$~1, $T_m$~Sex | 4 | 1584 | 1.1 | 0.3 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 1593 | 10.3 | 0.0 | 1.0 |
| 2010 | **$A_{max}$~1, $T_m$~Sex** | **4** | **1559** | **0.0** | **0.5** | **0.5** |
| | $A_{max}$~Sex, $T_m$~1 | 4 | 1559 | 0.3 | 0.4 | 0.8 |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 1561 | 2.1 | 0.2 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 1573 | 14 | 0.0 | 1.0 |
| 2013 | **$A_{max}$~Sex, $T_m$~1** | **4** | **1458** | **0.0** | **0.4** | **0.4** |
| | $A_{max}$~1, $T_m$~Sex | 4 | 1458 | 0.4 | 0.3 | 0.8 |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 1459 | 1.5 | 0.2 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 1462 | 4.7 | 0.00 | 1.0 |
| 2015 | **$A_{max}$~1, $T_m$~Sex** | **4** | **1508** | **0.0** | **0.5** | **0.5** |
| | $A_{max}$~Sex, $T_m$~1 | 4 | 1509 | 0.9 | 0.3 | 0.8 |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 1510 | 2.1 | 0.2 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 1589 | 80.8 | 0.0 | 1.0 |
| 2016 | **$A_{max}$~1, $T_m$~Sex** | **4** | **1560** | **0.0** | **0.5** | **0.5** |
| | $A_{max}$~Sex, $T_m$~1 | 4 | 1561 | 0.8 | 0.3 | 0.8 |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 1562 | 1.7 | 0.2 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 1680 | 121.1 | 0.0 | 1.0 |
| 2017 | **$A_{max}$~Sex, $T_m$~1** | **4** | **1587** | **0.0** | **0.5** | **0.5** |
| | $A_{max}$~1, $T_m$~Sex | 4 | 1587 | 1.0 | 0.3 | 0.8 |
| | $A_{max}$~Sex, $T_m$~Sex | 5 | 1589 | 2.1 | 0.2 | 1.0 |
| | $A_{max}$~1, $T_m$~1 | 3 | 1639 | 52.7 | 0.00 | 1.0 |

that reported by Weimerskirch (2007), who analyzed trajectories from 34 seabird species and found that, at the population level, birds travel through similar zones toward feeding areas, although each individual shows some preference for specific sectors within them.

In all seasons, the sizes of the active use and core foraging areas of both males and females increased with increasing sample size until reaching an asymptote. This pattern indicates that precise results can be obtained with a limited number of tagged individuals. The interannual variability observed in use and foraging areas suggests that, to determine areas of activity, it may be more appropriate to maintain an adequate number of tagged individuals over the long term rather than tagging a very large number in only a few seasons. In any case, the number of males and females to be tagged will depend on previous evidence reporting differential space use—and/or behaviors that lead to it—between sexes.

In our case, under the 1% criterion, we found that

**Table 6.** Estimated parameters of the Michaelis–Menten model that showed the best fit for each year to predict core foraging area as a function of sample size for female and male Imperial shags (*Leucocarbo atriceps*) at the Punta León colony. The confidence interval [Min–Max] is indicated. Significant comparisons between sexes for the parameters $A_{max}$ and $T_m$ are shown in bold.

| Year | $A_{max}$ | | $T_m$ | |
|---|---|---|---|---|
| | **Female core foraging area (km²)** | **Male core foraging area (km²)** | **Female core foraging area (*n* of animals)** | **Male core foraging area (*n* of animals)** |
| 2008 | 256 [158-354] | 263 [187-340] | 15 [6-23] | 14 [8-20] |
| 2009 | **244 [151-337]** | **168 [120-217]** | 16 [7-25] | 11 [6-16] |
| 2010 | 238 [139-337] | 230 [152-309] | **18 [8- 28]** | **15 [7- 22]** |
| 2013 | **211 [98-324]** | **154 [103-206]** | 21 [6-36] | 15 [7-22] |
| 2015 | 206 [139-274] | 205 [106 -305] | **14 [7-20]** | **20 [7-33]** |
| 2016 | 196 [154-239] | 171 [123 -220] | **9 [5-12]** | **12 [7 -17]** |
| 2017 | **245 [178-313]** | **197 [131- 263]** | 13 [7-18] | 12 [6-19] |
| Mean | 228 [196-256] | 199 [103-187] | 15 [9-21] | 14 [11-20] |

25 and 32 tagged individuals per sex (i.e., approximately 0.4–0.5% of the total number of breeding adults of each sex in the colony) would be necessary to estimate the sizes of the active use and core foraging areas, respectively, with that level of precision. The numbers of animals to be tagged are reduced to less than half (i.e., 10 and 12, for use and foraging areas, respectively) if a precision level of 5% is considered acceptable for determining area size. The choice of which precision level to adopt will depend on the accuracy required by the conceptual and/or experimental framework of the research and, ultimately, on the time and financial resources available. Conceptually complex questions may require the 1% criterion, that is, the highest level of precision, and therefore a larger number of tagged birds. However, for exploratory studies or for identifying areas of importance (e.g., IBAs), the 5% criterion would allow optimization of time and financial resources allocated to device acquisition without substantially compromising the representativeness of the study.

It is important to consider that the results obtained in this study focus on a particular period of the breeding season and on a specific site; therefore, extrapolation to other sites and/or periods of the same species or to other similar species should be made with caution. Likewise, results obtained from estimates for sample sizes greater than the reference sample size should be interpreted carefully. The reliability of the model describing the relationship between area size and number of individuals decreases once the sample size used in the present study is exceeded (20 Imperial shags for the population-level analysis and 10 for the sex-specific analysis). Extrapolations beyond these values are based on model predictions, which involve a higher degree of uncertainty (Colwell et al. 2012).

The implementation of GPS devices and related technologies in wildlife studies does not always include an adequate assessment of their impacts on animal welfare (Quintana et al. 2024). In this context, the careful planning of instrumentation strategies constitutes not only a measure of scientific efficiency—by optimizing resources and reducing sampling and analysis time—but also a commitment to fundamental ethical principles by avoiding excessive and unnecessary handling. This study seeks to contribute to the development of more responsible scientific practices by promoting the conscious and justified use of biologging devices.

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# STATUS OF NEARCTIC AND AUSTRAL MIGRATORY BIRDS IN THE BRAZILIAN STATE OF ACRE, SOUTHWESTERN AMAZON: INSIGHTS FROM CITIZEN SCIENCE CONTRIBUTIONS

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**ABSTRACT:** Migratory birds undertake seasonal movements between breeding and non-breeding areas in search of favorable climatic and food conditions. In South America, two major migratory systems are recognized: Nearctic and Austral. The Brazilian state of Acre, located in the southwestern Amazon, serves as a strategic stopover for both groups, yet increasing anthropogenic pressures threaten these corridors. Understanding migration dynamics is therefore essential for conservation planning. This study analyzed temporal patterns of Nearctic and Austral migratory bird species in Acre and assessed their degree of temporal overlap. Data was obtained from citizen science platforms, with photographic records filtered by species and month and visualized through heatmaps. Records were classified into reproductive and non-reproductive months, and differences tested using the non-parametric Mann-Whitney U test ($p < 0.05$). A total of 1554 images representing 61 migratory species (31 Nearctic and 30 Austral) were analyzed. Solitary Sandpiper (*Tringa solitaria*) showed the highest frequency of records among Nearctic migrants, whereas Vermilion Flycatcher (*Pyrocephalus rubinus*) prevailed within the Austral group. Phenological analysis revealed distinct seasonal windows: Nearctic migrants occurred mainly from September to March, whereas Austral migrants were recorded from March to September, with minimal overlap. Some species, such as Chivi Vireo (*Vireo chivi*) and Crowned Slaty Flycatcher (*Empidonomus aurantioatrocristatus*), were observed nearly year-round, suggesting complex strategies including partial migration or coexistence of resident and migratory populations. These findings highlight Acre's role as a dynamic migratory corridor and demonstrate the value of citizen science in monitoring avian biodiversity in remote regions, reinforcing its importance for conservation strategies.

**KEYWORDS:** *Amazonia, birds, citizen science, migratory route*

Migratory birds undertake seasonal movements between breeding and non-breeding areas, often spanning vast geographic distances and ecological zones. These movements are driven by the need to optimize access to resources such as food, shelter, and suitable climatic conditions (Saunders et al. 2025). In South America, two major migratory systems are recognized: the Nearctic and the Austral flyways (Sick 1983, Stotz et al. 1992, Chesser 1994, Jahn et al. 2004, Alves 2007). Nearctic migrants breed in North America, primarily in Canada, the United States, and northern Mexico and migrate southward to wintering grounds across Central and South America, including Brazil (Stotz et al. 1992, Valente et al. 2011, Humple et al. 2020). Conversely, Austral migrants originate from southern regions of South America, such as Argentina, Chile, and Uruguay, and travel northward during the austral winter to reach tropical and subtropical zones

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(Sick 1983, Chesser 1994, Cestari 2015).

The Brazilian Amazon, particularly the state of Acre, serves as an important stopover and destination for both Nearctic and Austral migratory species (Guilherme 2012, 2016). These birds rely on a mosaic of habitats for resting, feeding, and refueling during their journeys. However, increasing anthropogenic pressures such as deforestation, urban expansion, and climate change pose significant threats to the integrity of these migratory corridors and the survival of the species that depend on them (Saunders et al. 2025).

Understanding the spatial and temporal dynamics of migratory routes is essential for developing effective conservation strategies. Migratory connectivity, which links breeding and non-breeding populations across regions, is a critical concept in identifying priority areas for habitat protection and restoration (Saunders et al. 2025).

Citizen science initiatives have become increasingly vital for monitoring migratory bird populations, particularly in regions with limited scientific coverage, while also enabling accurate predictions of migratory routes (Fuentes et al. 2023). Platforms such as eBird have generated extensive datasets that allow researchers to assess migration timing, distribution, and habitat use across remote areas in North America, Europe, Africa, Asia, and Oceania (Sullivan et al. 2014). For example, eBird data have been used to evaluate stopover ecology and migration phenology in boreal and Arctic regions of North America, where traditional surveys are logistically challenging (La Sorte et al. 2016). In Africa, citizen science records have contributed to the monitoring of Palearctic migrants in Kenya, providing insights into habitat use and changes in geographical distribution over time (Nussbaumer et al. 2024). In Oceania, citizen science has revealed a hidden migratory diversity in eastern Australia, far greater than previously recognized, including species with little legal protection (Shi et al. 2025). Collectively, these contributions demonstrate how citizen science can complement professional monitoring, enabling robust, large-scale assessments of population trends and habitat use in remote areas worldwide. Furthermore, citizen science initiatives have proven valuable for monitoring migratory bird populations in regions such as Acre, where formal scientific coverage may be limited (Guilherme 2012, 2016). These efforts help fill critical data gaps and support large-scale assessments of population trends and habitat use (Humple et al. 2020, Barbosa et al. 2021).

In this context, the primary objective of this study is to assess the seasonal dynamics of migratory flow of Nearctic and Austral bird species in the Brazilian State of Acre. Specifically, the study aims to determine the temporal patterns of occurrence of these migratory groups and to evaluate whether Nearctic and Austral species co-occur (sympatry) in the region or utilize the area during distinct periods, thereby revealing temporally segregated migratory strategies.

## METHODS

### Study area

The study focused on the territorial boundaries of the Brazilian state of Acre (Fig. 1). The state of Acre covers an area of 164,221.36 km², sharing international borders with Peru and Bolivia, and national borders with the states of Amazonas and Rondônia (Acre 2015). The territory is traversed by two major rivers: the Juruá, which flows through the western region and the Purus, which crosses the central area (Guilherme 2012, 2016). The climate is humid equatorial, with annual rainfall ranging from 1400 to 3000 mm, predominantly concentrated between November and April (Acre 2014). The predominant vegetation consists of dense *terra firme* forest, with areas dominated by bamboos (*Guadua* sp.) and palms, as well as seasonally flooded várzea forests that develop along the alluvial plains of the main rivers (Daly & Silveira 2008, Guilherme 2016). The eastern region of the state, where the capital Rio Branco is located, is the most densely populated and experiences the highest anthropogenic pressure, with significant impacts on natural ecosystems due to urban expansion, agriculture, and extractive activities (Acre 2015).

### Data collection

The documentation of migratory birds within the state of Acre was conducted through the retrieval of species images from three major citizen science platforms: (a) iNaturalist (2025); (b) WikiAves (2025); and (c) eBird (2025). These platforms host thousands of photographs contributed by over 50,000 volunteers. For our survey, we employed the advanced search tools provided by each platform to filter images of Nearctic and Austral migratory bird species recorded in Acre. We restricted our search exclusively to photographs of specimens, while videos, audio recordings, and indirect evidence such as images of tracks or feathers were not screened. To ensure consistency with established records, we relied on the dataset presented in Table 3 by Guilherme (2016), which lists

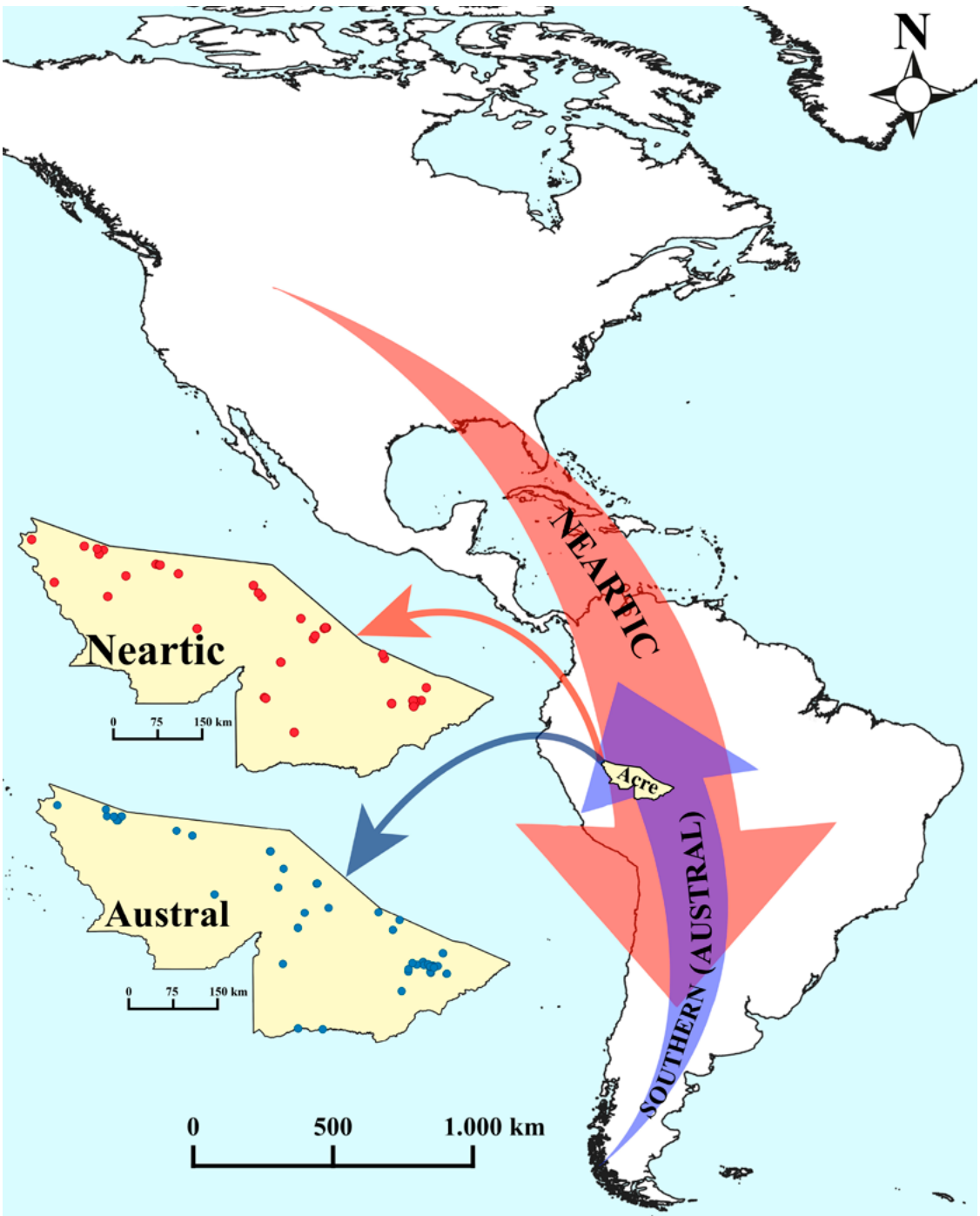


**Figure 1.** Geographic location of the Brazilian state of Acre in relation to the main migratory flyways of Nearctic and Austral bird species across The Americas. The detailed maps of Acre show the sites where at least one migratory species was recorded. Red points (Nearctic) and blue points (Austral) indicate the locations where at least one image of a migratory species was registered. Major arrows indicate the migratory flows between hemispheres, emphasizing Acre's strategic role as an ecological corridor for migratory birds.

all Nearctic and Austral migratory species previously documented in the state of Acre over a 65-year period, between 1951 and 2016. By using this comprehensive reference, our image selection was restricted to the exact number of species reported in that study, thereby providing a reliable basis for analysis.

### Data curation

The selected photographs were sorted chronologically, from the oldest to the most recent records. Subsequently, we screened the retrieved images to determine their eligibility for inclusion in our dataset. Each record's eligibility was established by the bird's confirmed presence, verified through photographic evidence within the state boundaries, supported by municipal-level location data. Each valid record was entered as a row in an Excel spreadsheet, which was later used to generate comparative graphs illustrating species presence across the state. Images were organized by species name and annotated with metadata including photo URL, source platform, contributor, date, municipality, specific locality, geographic coordinates, habitat type, and additional observations. Some images were excluded due to redundant information (identical contributor, date, and location). The earliest photographs retrieved date back to 2008 and extend through to July 2025. This temporal range provides a valuable longitudinal perspective on the occurrence and distribution of migratory bird species within Acre, enabling the identification of patterns and potential shifts in migratory behavior over time, particularly among the most frequently photographed species across successive years. We surveyed 61 migratory species comprising 30 Austral and 31 Nearctic species (see Table 3 by Guilherme 2016). Scientific nomenclature follows that of AviList (AviList Core Team 2025).

### Data processing

*Phenology*: To visualize and gain a general understanding of the temporal distribution of Nearctic and Austral migrants in Acre, a heatmap was constructed using RStudio software (version 12.1; R Core Team. 2024). We visualized the occurrence of different species across the months over the past 16 and a half years (2008 to July 2025). The data were organized into a record matrix, representing the number of monthly images for each species. The chronological ordering of months was manually defined to ensure temporal consistency. The heatmap was generated using a dedicated function, which was employed to represent each cell of the matrix. The fill scale was defined using a color palette ranging from light tones (indicating minimum records counts) to dark tones (indicating maximum records counts). The interpolated gradient allowed for a smooth transition between minimum and maximum values, enhancing the visual perception of intensity patterns. All images of each species obtained within the state were classified into reproductive and non-reproductive months to evaluate seasonal variation in species occurrence. The categorization of migratory species into reproductive and non-reproductive periods was based on Birds of the World (Billerman et al. 2026). This classification enabled the identification of months associated with documented reproductive activity versus those without evidence of breeding. Statistical differences in the number of images recorded during reproductive and non-reproductive months were tested using the non-parametric Mann-Whitney U test, with a threshold of $p < 0.05$ considered significant (Nachar 2008). The analysis was conducted for 45 species represented in the heatmap, ensuring comprehensive coverage of the migratory taxa included in the dataset. The statistical procedures were performed using the software PAST version 3.24 (Hammer et al. 2001). The dataset used in this study is available on the Mendeley Data platform (Pereira et al. 2026).

*Minimizing bias in long-term time series*: Species presence and absence can allow for inferring migratory patterns within the region (Somveille et al. 2013, Dennis et al. 2025). However, incorporating the number of photographic records per month adds a valuable dimension, potentially reflecting fluctuations in the relative abundance of individuals throughout the year. While we acknowledge the inherent bias in citizen science data, particularly the opportunistic nature of observations that may increase during periods of heightened field activity (Zhang et al. 2025), for example, during the dry season in Acre when rural areas become more accessible via roads, we consider that long-term datasets can mitigate these effects and allow for the detection of robust ecological trends (Strien et al. 2013, Kelling et al. 2019, Johnston et al. 2021). Moreover, comparative analyses between platforms such as eBird and iNaturalist have demonstrated consistent seasonal patterns of bird occurrence, despite differences in user profiles and data collection methods (Carroll et al. 2025). Therefore, graphical representations of monthly records for migratory species are likely to reflect actual population dynamics rather than merely observer effort (Koh & Opitz 2024). This approach strengthens our ability to identify cycles of arrival, residency, and departure,

and highlights potential temporal overlap between Austral and Nearctic migrants in Acre.

## RESULTS

A total of 1554 images were screened (1540 included and 14 excluded). Of the included images, 495 (32.1%) were taken between November and April, corresponding to the rainy season, whereas 1045 (67.9%) were taken between May and October, corresponding to the dry season. The dataset comprised 675 Nearctic migrants and 879 Austral migrants. Among the 31 Nearctic migratory species previously recorded in Acre, 10 (Blue-winged Teal, *Spatula discors*; Baird's Sandpiper, *Calidris bairdii*; Least Sandpiper, *Calidris minutilla*; Grey-cheeked Thrush, *Catharus minimus*; Black-billed Cuckoo, *Coccyzus erythropthalmus*; Connecticut Warbler, *Oporornis agilis*; Barn Swallow, *Hirundo rustica*; Laughing Gull, *Leucophaeus atricilla*; Wilson's Phalarope, *Phalaropus tricolor*; and Sand Martin, *Riparia riparia*) had no images recorded on any of the platforms. Three species (Swainson's Hawk, *Buteo swainsoni*; Stilt Sandpiper, *Calidris himantopus*; and Olive-sided Flycatcher, *Contopus cooperi*) were recorded exclusively on one platform (WikiAves), while Broad-winged Hawk (*Buteo platypterus*), Buff-breasted Sandpiper (*Calidris subruficollis*), and Summer Tanager (*Piranga rubra*) were found on only Wikiaves and iNaturalist platforms. Among the 31 Nearctic migrant species analyzed, 14 showed low or no representation across the platforms. Of these, six species had no records at all: Sick's Swift (*Chaetura meridionalis*), Southern Tropical Pewee (*Contopus cinereus*), Scissor-tailed Nightjar (*Hydropsalis torquata*), Greenish Elaenia (*Myiopagis viridicata*), Subtropical Doradito (*Pseudocolopteryx acutipennis*), and Blue-and-white Swallow (*Pygochelidon cyanoleuca*). Three species (Nacunda Nighthawk, *Chordeiles nacunda*; White-crested Elaenia, *Elaenia albiceps*; and Pantanal Snipe, *Gallinago paraguaiae*) were recorded on only Wikiaves platform, and five (Small-billed Elaenia, *Elaenia parvirostris*; Bran-colored Flycatcher, *Myiophobus fasciatus*; Southern Martin, *Progne elegans*; White-throated Kingbird, *Tyrannus albogularis;* and Ash-colored Cuckoo, *Coccycua cinerea*) were found only on Wikiaves and eBird platforms.

### Most Frequently Photographed Species

The photographic records of migratory birds in Acre show that among the Nearctic migrants, Solitary Sandpiper (*Tringa solitaria*) was the most photographed, with 157 images, recorded year-round but more frequent from August to December (Fig. 2A). Pectoral Sandpiper (*Calidris melanotos*) had 89 records, present from August to December (Fig. 2B). Eastern Wood Pewee (*Contopus virens*) appeared in nearly all months, peaking in November with 83 images (Fig. 2C). Finally, Eastern Kingbird (*Tyrannus tyrannus*) had 80 records, occurring from September to May and absent from June to August (Fig. 2D). Among the Austral migrants, Vermilion Flycatcher (*Pyrocephalus rubinus*) was the most photographed, with 239 images, occurring from April to October (Fig. 2E). Fork-tailed Flycatcher (*Tyrannus savana*) had 100 records, present during the rainy season (Jan-Apr) and the dry season (Jul-Oct; Fig. 2F). Crowned Slaty Flycatcher (*Empidonomus aurantioatrocristatus*) accounted for 96 images, occurring from February to November and absent only in Dec-Jan (Fig. 2G). Chivi Vireo (*Vireo chivi*) totaled 80 records, present from March to November and in January, absent in Dec-Feb (Fig. 2H).

### Phenology

The heatmap revealed a distinct migratory pattern with some overlap between Nearctic and Austral migratory bird species (Fig. 3). Nearctic species typically arrive in the state of Acre during the second half of the year, between September and October, and depart by March. In contrast, Austral species begin arriving in March and April, remaining until September or October (Fig. 3). The Mann-Whitney U test revealed statistically significant differences in temporal occurrence patterns for 47.6% of Nearctic migrants (Fig. 3). In contrast, among austral migrants only 8.3% showed significant differences, although two species (Variegated Flycatcher, *Empidonomus varius,* and Chivi Vireo) were at the threshold of statistical significance (Fig. 3).

## DISCUSSION

Migratory birds from both Austral and Nearctic regions exhibit seasonal movements toward northern South America, including the state of Acre, in response to favorable climatic and ecological conditions. This explains their year-round presence in the region. During the Austral autumn and winter, southern South America experiences colder temperatures and reduced food availability, prompting Austral species to move northward (Joseph 1996, Jahn et al. 2004). Similarly, Nearctic species depart from temperate North America during its fall and winter months, seeking warmer climates and richer foraging grounds in the tropics (Silveira et al. 2021, El Hindi

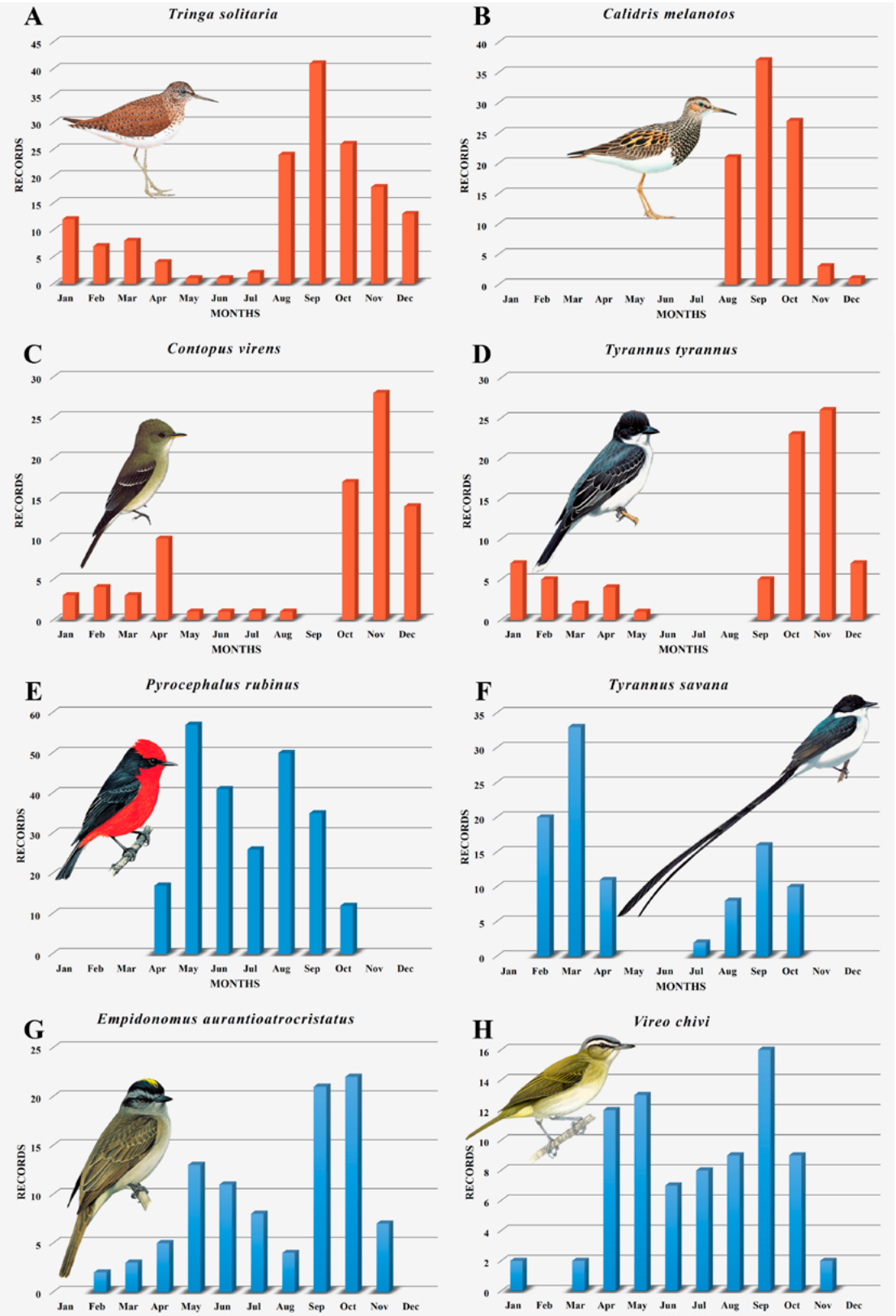


**Figure 2.** Temporal distribution of the four most frequently photographed Austral and Nearctic migratory bird species in the state of Acre between 2008 and July 2025. Records for A-D Nearctic and E-H Austral birds. Credits for bird illustrations: Farmer et al. (2020), Jahn & Tuero (2020), Kirwan (2020), Moskoff (2020), Murphy & Pyle (2020), Robb (2020), Watt et al. (2020), and Ellison et al. (2021).

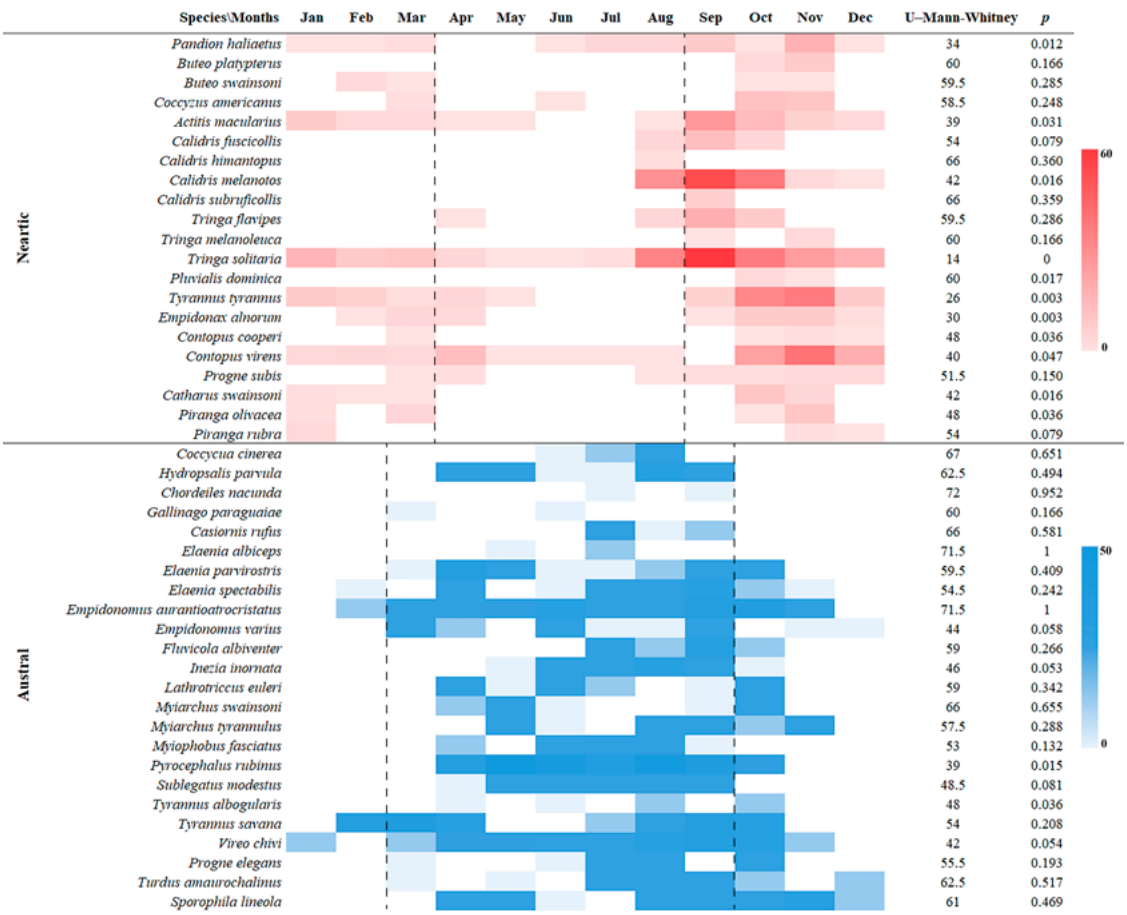


**Figure 3.** Heatmap of the migratory phenology of Nearctic and Austral bird species in the state of Acre between 2008 and July 2025. Color intensity represents the monthly frequency of photographic records for each species. Dashed lines indicate periods of minimal temporal overlap between Nearctic and Austral migratory species, highlighting distinct seasonal patterns of occurrence in the region. The last two columns show the Mann-Whitney U test statistics and the corresponding *P*-value.

et al. 2023). The investigation of this phenomenon in the Neotropical region has been greatly facilitated by the extensive databases provided by citizen science platforms, which enable research across large geographic areas without major logistical challenges or high operational costs (Schubert et al. 2019, Jahn et al. 2020). Results have revealed consistent migratory patterns for birds across different regions of South America similar to those observed in the present study (Schubert et al. 2019, Barbosa et al. 2021, Thibaudier et al. 2025). Although a potential bias of working with images in Acre is that more birdwatchers visit the state during the drier months, reflected in the fact that greater than 50% of the images were obtained in this period, it was nevertheless possible to detect a clear migratory pattern of Nearctic species, which occur in the state during the rainy season. We believe this was feasible because the dataset encompassed a long sampling period of more than 15 years, as previously discussed regarding the biases inherent to citizen science data. An additional bias in our study may explain why Vermilion Flycatcher and Fork-tailed Flycatcher accounted for the highest number of photographs. Both species are migratory birds associated with open habitats and are known to use urban and peri-urban environments during their seasonal movements (Jahn et al. 2016, Thibaudier et al. 2025). This ecological behavior increases their visibility and accessibility to observers, thereby facilitating the documentation and acquisition of images compared to species that remain restricted to forested habitats.

Among Nearctic birds, Solitary Sandpiper was the only Scolopacidae species recorded in Acre throughout all months of the year. Nevertheless, its migratory pattern proved to be statistically significant, given that during the breeding months of May and June (Moskoff 2020) only a single image was documented in each month within the boundaries of Acre over the past 17 years, in sharp contrast to the considerably higher

number of records obtained during the non-breeding months (Fig. 3). This shorebird is commonly seen on the Campus of the Federal University of Acre, foraging along the edges of ponds either alone or in small flocks (Guilherme 2001, 2016). Color-banded individuals observed on campus in subsequent years suggest that they remain locally for more than one summer (EG pers. obs.). These birds breed in high-latitude regions of the Northern Hemisphere and, for the most part, migrate along coastal areas, where sites with large concentrations of individuals are found (Campos et al. 2008, Valente et al. 2011, Somenzari et al. 2018). The Spotted Sandpiper (*Actitis macularius*) was present in Acre throughout 10 months, except for June and July, which correspond to the peak breeding season of the species in temperate North America, particularly in the United States (Reed et al. 2020). The other shorebirds (e.g., *Calidris* sp.) were present in Acre only during the expected wintering period in Brazil, between the months of August and December (Fig. 3; Valente et al. 2011, Somenzari et al. 2018). The Eastern Wood Pewee migrates from eastern North America, through Central America, to winter in the western Amazon (Watt et al. 2020) and may also reach regions in Central Brazil (Somenzari et al. 2018). Watt et al. (2020) identifies two migration periods: one in spring and the other in autumn, which explains its presence in Acre during almost every month of the year, except September (Fig. 3). The Eastern Kingbird breeds in the northern United States and Canada and migrates to the forests of South America during the boreal winter (Murphy & Pyle 2020). This species undergoes both spring and autumn migrations (Murphy & Pyle 2020), like the Eastern Wood Pewee, which explains its presence in Acre from January to April and from September to December, with a peak in records during October and November, coinciding with the winter months in the breeding sites.

Some species, such as Vermilion Flycatcher, occupy a wide range across South, Central, and North America, encompassing 12 subspecies, some of which are resident while others are migratory (Carmi et al. 2016). The Austral migrant that reaches the state of Acre is the nominal subspecies: *P. r. rubinus* (Carmi et al. 2016, Canassa 2022, Thibaudier et al. 2025). According to Sick (1983), *P. r. rubinus* initiates its migratory activity around mid-January, departing from Argentina towards northern South America. Recent citizen science data indicate that this species winters between May and August, with northward migration occurring in March and April, and southward return migration between September and October (Thibaudier et al. 2025). The presence of Vermilion Flycatcher in the state of Acre from April to October is consistent with these findings. Among austral migrant species, this was the one that exhibited the clearest migratory pattern, with records in Acre restricted to the wintering months (Fig. 3). Data indicated that the Southern Fork-tailed Flycatcher migrates to Acre during two distinct seasons: the rainy season and the dry season (Fig. 2F). According to Jahn et al. (2016), individuals of this species exhibit two main migratory periods: an autumnal migration involving birds that breed in southeastern Brazil and migrate to northern South America, and a spring migration involving individuals that breed in Argentina and migrate to northwestern South America. This dual pattern helps explain the two migratory waves observed in Acre: one occurring from February to April, and another from July to October, corresponding to the timing of post-breeding and pre-breeding movements within South America (Jahn et al. 2013, Jahn et al. 2016). These intra-tropical migrations reflect the broader diversity of migratory strategies among Neotropical Austral migrants, which often winter north of their breeding areas and may use multiple stopover or overwintering sites (Chesser 1994, Jahn et al. 2004). The Crowned Slaty Flycatcher and Chivi Vireo have been photographed in the state of Acre throughout nearly the entire year (Fig. 3). According to Jahn et al. (2004), the Crowned Slaty Flycatcher exhibits a type of migration known as leapfrog partial migration, in which some individuals of the population are migratory while others are resident. We believe that this pattern also explains the year-round presence of Chivi Vireo in Acre.

### Phenology

This long-term dataset allowed us to identify distinct seasonal windows of occurrence for each migratory group, with some overlap in their periods of peak activity. Nearctic migrants typically arrive in Acre during the second half of the year, with a concentration of records between September and October. These species remain in the region until March, after which their presence declines sharply. This pattern aligns with their migratory routes from North America to South America during the boreal winter. In contrast, Austral migrants begin arriving in Acre in March and April, coinciding with the end of the rainy season, and remain until September or October. Their migratory cycle reflects movements within South America, often between southern breeding grounds and northern non-breeding areas.

Seasonal statistical differences were more evident among Nearctic species. This indicates a clear migratory pattern in the study region, where the likelihood of observing these species increases significantly during non-breeding months. For certain Nearctic species in which no significant pattern was detected, we attribute this outcome to the low number of available records in the surveyed platforms, such as Swainson's Hawk, Stilt Sandpiper, Buff-breasted Sandpiper, Greater Yellowlegs (*Tringa melanoleuca*), and Summer Tanager, all represented by fewer than ten images during the sampling period. Among austral species, no significant seasonal differences were observed for most taxa. In some cases, this was also due to limited sampling, as with Pantanal Snipe, Nacunda Nighthawk, Ash-colored Cuckoo, White-crested Elaenia, and Rufous Casiornis (*Casiornis rufus*). However, the absence of seasonal statistical differences may be more convincingly explained by the presence of resident populations that remain in the region year-round, as documented for Chivi Vireo and Crowned Slaty Flycatcher (Jahn et al. 2004, Schulenberg et al. 2007, Somenzari et al. 2018), or by species that exhibit more complex migratory patterns, such as two distinct migratory periods, as observed in Fork-tailed Flycatcher (Jahn et al. 2016). Another plausible explanation relates to the physical condition of individuals: juveniles or weakened birds may be unable to initiate return migration after the breeding season, remaining longer in the area to feed and accumulate energy reserves. These individuals typically resume migration in the following season once they are physically prepared. Confirmation of this pattern will require systematic field studies capable of monitoring both migratory populations and individuals that fail to return to breeding areas. If validated, such behavior would have important implications for migratory ecology and conservation strategies, highlighting the need to protect habitats used beyond traditional migratory windows (Jahn et al. 2020).

## CONCLUSION

The state of Acre serves as a seasonal refuge and strategic corridor for migratory birds, sustaining ecological connectivity across The Americas. Nearctic migrants, particularly shorebirds, use the Amazon Basin's rivers and floodplains as vital stopover and wintering sites during their southward journeys (Linscott et al. 2024), while Austral migrants from southern South America depend on Acre's forests and wetlands during the non-breeding season. Acre's warm and humid climate corresponds to the ecological requirements of some Austral migrant species adapted to tropical lowland conditions (Joseph 1996), reinforcing its role as a refuge within the Amazon Basin (Valente et al. 2011, Guilherme 2012, 2016). The alternating presence of these two migratory groups, with limited temporal overlap, reduces interspecific competition and highlights Acre's dual importance as a hemispheric convergence zone. The degradation of Acre's wetlands, riparian zones, floodplain forests, and *terra firme* upland forests would simultaneously affect both Nearctic and Austral migratory systems, underscoring the urgency of integrating Acre into transnational conservation frameworks that safeguard biodiversity and ecological resilience across the continent. Acre's conservation is therefore fundamental not only for sustaining migratory connectivity but also for ensuring the long-term resilience of the Amazon as a whole (Leal Filho et al. 2025).

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# TIME–ACTIVITY BUDGETS OF THREE COOT SPECIES IN A RELICT OF HUMAN-MODIFIED COASTAL WETLANDS IN SOUTHEASTERN BUENOS AIRES PROVINCE

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**ABSTRACT:** The amount of time individuals allocate to different behavioral activities influences their survival and reproductive success. In urban wetlands and lagoons, pressure from various anthropogenic activities affects multiple components of these ecosystems, including waterbirds. This study characterized the time–activity budgets of three sympatric coot species in an anthropogenic urban lagoon environment. Although surveys were conducted at the beginning of the birds' breeding season, no breeding-related behaviors (e.g., courtship, nesting) were observed, suggesting that the studied populations may have consisted of juvenile or non-breeding individuals. A total of 636 focal observations were conducted, during which more than ten distinct behaviors were recorded. Overall, and across all three species, time allocated to foraging and swimming jointly accounted for more than 80% of the total time budget. Regarding foraging techniques, feeding both at the water surface and outside the water column (i.e., within vegetated areas) predominated. The average distribution of time allocated among activity categories varied among species and across time periods of the day. Although these results are descriptive in nature, they are consistent with those reported for other coot species inhabiting different regions. Behavioral studies provide insight into fundamental aspects of the biology of species and are a key tool for proposing management measures aimed at ensuring their conservation in urban ecosystems exposed to multiple anthropogenic impacts.

**KEYWORDS:** *Argentina, behavior, Buenos Aires province, Fulica sp., urban lagoons*

Wetlands are considered one of the most relevant ecosystems globally, characterized not only by supporting high biodiversity, but also by the multiple ecosystem services they provide, such as water purification, support for recreational activities, and environmental education, among others (Ghermandi et al. 2010, Ramsar 2016, Alikhani et al. 2021). Wetlands are grouped into three main categories: marine-coastal, inland, and artificial wetlands (Ramsar 2016). Within these categories, we can identify so-called urban wetlands, which are located within urban or peri-urban areas and can be of natural or artificial origin (Palta et al. 2017, Alikhani et al. 2021). These types of wetlands are often among the most affected, partly due to pressure exerted by multiple human activities that result in habitat degradation, water pollution, biodiversity loss, and the introduction of exotic or invasive species, among others (Alikhani et al. 2021). Urban wetlands, as well as other water bodies (e.g., artificial urban lagoons), are widely used by various taxa, such as fish, amphibians, reptiles, mammals, and birds (Schnack et al. 2000, De Marco et al. 2011, Hassall et al. 2014, Alikhani et al. 2021). With respect to birds, so-called waterbirds are usually the most conspicuous in these environments (e.g., families Anatidae, Rallidae, Podicipedidae; McKinney et

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al. 2011, Murray et al. 2013, Hassall 2014). This group of birds may use these water bodies permanently, as well as during some stage of their life cycle (e.g., breeding period, wintering), or they may make partial use of them during migration (Traut & Hostetler 2004, Tallei et al. 2021, Xie et al. 2022). Therefore, these water bodies function as feeding, resting, shelter, and even breeding sites for many waterbird species (Traut & Hostetler 2003, Murray et al. 2013, Alikhani et al. 2021).

Birds have a limited amount of time throughout the day to carry out their activities; the allocation of time among different activities is commonly known as a time budget (Barnard 1980). The study of time budgets devoted to daily activities provides valuable information on how individuals perform different activities in order to improve their reproductive success (Ryan & Dinsmote 1979, Stephens et al. 2007, Dunbar et al. 2009). Among the diversity of daily activities an individual may perform, feeding plays an essential role, directly influencing the time allocated to activities such as resting, preening, and even reproduction, among others (Illius et al. 2002, Dunbar et al. 2009, Rose et al. 2022, Mukherjee et al. 2023). It is crucial to emphasize that time allocation to a particular behavior can vary significantly both at hourly and seasonal scales (Mukherjee et al. 2023). At the hourly scale, for example, time allocated to feeding is usually concentrated in the early and late hours of the day. This may be because birds thereby avoid both thermal stress and human disturbance, while resting may predominate during midday (Döpfner et al. 2009). Therefore, understanding these hourly patterns makes it possible to evaluate the efficiency with which waterbirds use their habitats.

With regard to seasonal variation, during the breeding period, activities such as egg laying and chick care become more relevant, modifying time budgets (Ryan & Dinsmote 1979, Döpfner et al. 2009, Mukherjee et al. 2023). Prior to the onset of the breeding period, there is an increase in energetic needs or the accumulation of reserves, so waterbirds may increase consumption rate, select food items of higher energetic quality, invest more daily time in feeding, and/or reduce energetic expenditure (Stephens et al. 2007, Newton 2010). In contrast, during the non-breeding period, many waterbirds tend to invest more time in activities related to resting and swimming (Döpfner et al. 2009, Mukherjee et al. 2023).

In addition to temporal variation, the coexistence or sympatry of species using the same resource, for example, an urban wetland, as in this study, may generate the need for niche differentiation (Murray et al. 2013, Mukherjee et al. 2023). In this way, it is expected that sympatric species, through behavioral segregation, minimize competition, resulting in different time budgets and resource use among species (Mukherjee et al. 2023). Therefore, quantifying and comparing time budgets of different behaviors among species is relevant for evaluating coexistence in anthropized environments (Murray et al. 2013, Hassall 2014, Rose et al. 2022, Mukherjee et al. 2023).

In Argentina, many ecosystems along the maritime coast are included within several wetland regions (e.g., Cuenca del Plata, Pampas, and Patagonian Coastal Zone; Secretaría de Ambiente y Desarrollo Sustentable de la Nación 2006). Among these, urban wetlands stand out, some of which contain water bodies permanently throughout the year. Among the most frequent and abundant waterbirds that use these environments are coots (*Fulica* sp., family Rallidae; Di Giacomo et al. 2007, González Trilla & Blanco 2017). These are waterbirds considered mostly or primarily herbivorous, but they may occasionally include aquatic insects, mollusks, and even crustaceans in their diets (Draulans & Vanherck 1987, García et al. 2008, Olguín et al. 2013, Velásquez et al. 2019). In Argentina, the genus *Fulica* is represented by six species, of which the White-winged Coot (*Fulica leucoptera*), the Red-fronted Coot (*F. rufifrons*), and the Red-gartered Coot (*F. armillata*), the focus of this study, are widely distributed along their latitudinal distribution gradient, which includes other countries such as Chile and Uruguay (Narosky & Yzurieta 2010). These species have an extended breeding period of approximately eight to ten months, which begins, with slight variation depending on the area, during the austral spring (e.g., between August and September), with egg-laying peaks in the austral summer (e.g., between December and January; Silva et al. 2011, Salvador 2012, Echevarria et al. 2022, De la Peña 2025).

In Argentina, studies of coots have focused on reproductive biology (Salvador 2012, Echevarria et al. 2022), habitat use (Heimsath et al. 1993), and trophic ecology (García et al. 2008, Olguin et al. 2013), with a strong geographic bias, as most studies were conducted in the central and northern parts of the country. It is worth noting that, despite the studies mentioned above, there are few studies aimed at evaluating the time investment that different species of the genus *Fulica* devote to their daily activities. The general objective of this study was to establish a baseline and characterize the time–activity budgets of three sympatric coot species that, during the months coinciding

with the onset of the birds' breeding period, used a highly anthropized urban lagoon environment that is part of a wetland relic in the southeast of Buenos Aires Province, Argentina. The specific objectives of the present study were to quantify and compare, descriptively, for each coot species separately and among coot species, the time invested in different behavioral activities and feeding techniques (a) among different times of day (i.e., morning, midday, afternoon), and (b) throughout the day (i.e., all time periods combined).

## METHODS

### Study area

The study area encompassed the Punta Mogotes lagoon complex (38°03'S, 57°32'W), located in the Partido de General Pueyrredon, in southeastern Buenos Aires Province, Argentina. The lagoon complex consists of four shallow lagoons (< 2 m) connected to each other and arranged in an arc, parallel to the coastline. With an approximate length of 2.5 km, it is bounded to the north by the Reserva Natural del Puerto Mar del Plata (RNPMdP) and the Club Atlético Aldosivi sports grounds, it is bounded to the south by Punta Cantera, and along its extension it is bounded to the west by Avenida de los Trabajadores and to the east by the Punta Mogotes beach resort complex (Fig. 1). The lagoon complex, together with the RNPMdP, is considered a relic of coastal wetlands (Richeri 2011). Given the surrounding infrastructure, both in terms of residential housing and commercial establishments, as well as the layout of the Punta Mogotes resort, the aforementioned sports club, and the port of Mar del Plata, the study area is fully urbanized, with port, industrial, commercial, and tourism activities prevailing (De Marco et al. 2005). The lagoon complex supports an important diversity of flora and fauna, where a wide variety of vertebrates coexist (i.e., fish, amphibians, reptiles, mammals, and birds), with birds being the most diverse and conspicuous group (De Marco et al. 2005). Regarding the birds using the study area, some of the most frequently observed species are the three coot species under evaluation (i.e., White-winged Coot, Red-fronted Coot, Red-gartered Coot), several grebe species (e.g., *Podiceps major*, *Rollandia rolland*), ducks (e.g., *Anas flavirostris*, *A. georgica*), gulls (e.g., *Chroicocephalus maculipennis*, *Larus dominicanus*), and the domestic Graylag Goose (*Anser anser*; De Marco et al. 2011, Berón & Seco Pon 2024). The lagoons are interconnected, allowing free movement among them by the birds that use them. Due to their location, the lagoons are similarly exposed to the impact of anthropogenic activities, from Avenida de los Trabajadores, which runs along the entire western side with constant vehicle traffic throughout the day, to the pedestrian and vehicular promenade of the beach resort complex along the eastern side, which is used for various outdoor activities such as walking, running, and resting. Due to its proximity to the RNPMdP, declared a Municipal Reserve in 1990 (Municipal Ordinance No. 7927/90) and in 2014 a Provincial Natural Reserve with Mixed Defined Objectives—Botanical, Faunal, and Educational (Provincial Law No. 14688), as well as its high environmental value, the Punta Mogotes lagoon complex is listed as a locally protected area (Municipal Ordinance No. 11038/97). In turn, the approximately 4 km stretch of coastline where the Punta Mogotes resort is located, adjacent to the study area, is considered one of the Important Bird Areas in Buenos Aires Province (IBA BA12; Di Giacomo et al. 2007).

### Data collection

During August to November 2022, coinciding with the breeding period of coots in Argentina (De la Peña 2025), we conducted weekly observations on weekdays using 5-minute focal samples (i.e., 300 seconds;

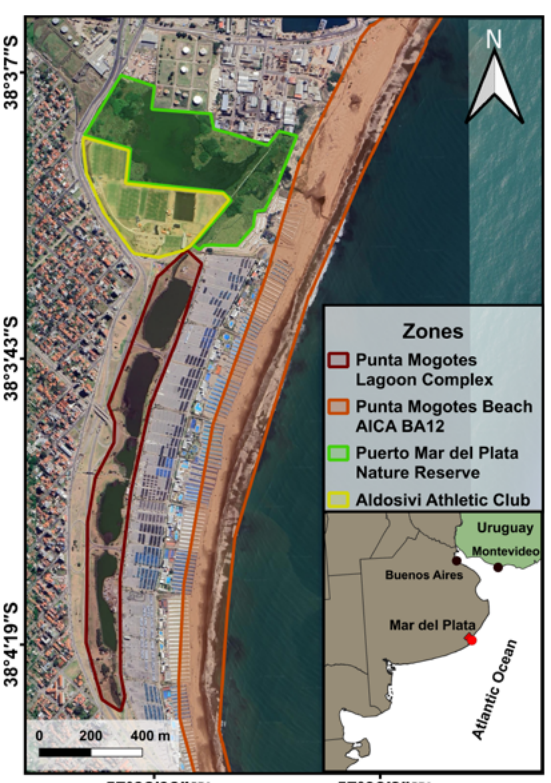


**Figure 1.** Study area. The study area is shown in relation to the coast of General Pueyrredón County, in the southeast of Buenos Aires Province, Argentina.

Altmann 1974) on three coot species inhabiting the study area. Focal observations of the three coot species were distributed across three time periods (local time, GMT -3): morning (8–10 h, $n$ = 255 focal observations), midday (11–13 h, $n$ = 193), and afternoon (14–16 h, $n$ = 188; Supplementary Material Table S1). For each time period, one of the water bodies within the lagoon complex was randomly selected. Within each, we selected a total of five individuals per species (i.e., White-winged Coot, Red-fronted Coot, Red-gartered Coot), on which focal observations were conducted, totaling 15 focal observations per species per day, evenly distributed across the three time periods considered. We conducted a total of 636 focal observations, corresponding to 53 h of recordings (White-winged Coot: $n$ = 214 focal observations, total recording time = 17.84 h; Red-fronted Coot: $n$ = 213, 17.75 h; Red-gartered Coot: $n$ = 209, 17.41 h; Supplementary Material Table S1). To reduce the probability of observing the same individual across time periods, we randomly rotated among lagoons for each time period analyzed. Although we did not have an estimate of population size for each coot species in the study area, the total number of individuals present in the lagoons was approximately fewer than 200 individuals per species. Observations and data collection were carried out at distances that did not disturb the animals' natural behavior (> 20 m), using binoculars (8 x 40) or a monocular (8 x 60) and a digital recorder. Two of the authors (MMH and MPB) conducted all observations. To minimize potential observer-related errors in recording behaviors, we conducted a behavioral assessment trial a few weeks prior to the study. For this, observers visited the study area and jointly observed the behaviors of the three species under evaluation, thereby standardizing the recognition of behaviors to be recorded.

The activities recorded during focal observations included: (a) 'self-maintenance', which included preening behaviors such as feather and/or bill cleaning and bathing; (b) 'resting', when the individual was observed stationary either in or out of the water; (c) 'swimming', when the individual was observed moving within the water; (d) 'paddling', when the individual moved across the water surface while flapping wings and legs; (e) 'flying'; (f) 'agonistic', any type of aggressive interaction with or without contact directed toward or by the focal individual; and (g) 'feeding'. Within this latter activity, feeding techniques were distinguished as follows: (1) 'surface feeding', defined as the ingestion and handling of food obtained from the water surface; (2) 'head–neck submerged', when the individual partially or totally submerges the head and neck; (3) 'diving', defined as total submersion of the focal individual, broken down into total time submerged and, when observed, time spent ingesting food obtained through this technique; (4) 'up-ending', a behavior in which the individual submerges half of the body, remaining upside down with legs extended vertically in the air (similarly to 'diving', this behavior was broken down into time submerged and, when observed, time spent ingesting food obtained through this technique); and (5) 'feeding outside the water body', defined as the ingestion and handling of food obtained from vegetated ground (i.e., outside the water body), following the criteria of Draulans & Vanherck (1987) and Ryma & Mouloud (2018).

### Data analysis

To characterize the time allocated by each coot species to different behaviors (recorded activities) and feeding techniques, we analyzed the recordings and quantified the total time (in seconds) devoted to each behavior during the 5-minute focal sampling period (i.e., 300 s), both at the daily scale (combined time periods) and intra-daily scale (i.e., morning, midday, afternoon). To account for the potential issue of pseudoreplication due to the unknown identity of sampled individuals, we used a data randomization protocol proposed by Garamszegi (2016). To implement this protocol, we randomly assigned an identity to each sample in the dataset (i.e., focal observation). This step assumes that the activity is highly repeatable and that coots consistently exhibit these activities. We repeated this process 1000 times and, in each simulation, calculated an overall mean for each activity category. We calculated this mean for each coot species, both for each time period analyzed and for the combination of them (Garamszegi 2016, Hernandez et al. 2021). To evaluate differences in daily activity budgets and feeding techniques both within and among species, we calculated, based on the simulations for each time period and their combination, an Overlap Index between the empirical distributions of the means of each behavioral category (see Pastore & Calcagní 2019, Hernandez et al. 2021). The Overlap Index (η) ranges between 0 and 1, where η = 0 indicates that empirical distributions are completely separate, whereas η = 1 indicates that empirical distributions are exactly the same. High values of the Overlap Index are interpreted as similarity in the probability distribution of time invested in a given activity or feeding technique, whereas low values indicate activities that differ in terms of time invested.

Data management and statistical analyses were performed using R, version 4.3.0 (R Development Core Team 2023). Simulations followed the supplementary material associated with Garamszegi (2016), while the Overlap Index was calculated using the '*Overlapping*' package version 2.2 (Pastore 2025).

## RESULTS

### Daily activity budgets

In general, throughout the entire study period and for the three species evaluated, the time invested in daily activities related to feeding and swimming together accounted for more than 80% of their time budgets. For White-winged Coots and Red-fronted Coots, unlike Red-gartered Coots, the percentage of time invested in feeding activities was greater than that invested in swimming (Fig. 2; Supplementary Material Table 2). Activities related to self-maintenance and resting together accounted for approximately 18% of the total time for the three coot species. The percentage of time invested in both activities was similar for Red-gartered Coots, whereas Red-fronted Coots invested a greater percentage of time in resting activities and White-winged Coots in self-maintenance activities (Fig. 2; Supplementary Material Table 2). For all species under study, agonistic interactions represented less than 0.5% of the time budget; these were generally non-contact interactions in which individuals were displaced a few meters without pursuit. On the other hand, behaviors such as flying and paddling were almost nonexistent (Supplementary Material Table 2). Regarding the different feeding techniques, and throughout the entire study period, both White-winged Coots and Red-fronted Coots invested a greater percentage of time consuming items at the surface outside the water (i.e., surface vegetation), followed by feeding at the water surface and consuming items obtained by diving. In the case of Red-gartered Coots, the percentage of time invested in the three feeding techniques mentioned above was similar (Fig. 2; Supplementary Material Table 3). The time invested in acquiring food through partial body immersion and head–neck submergence techniques was low and, combined and for all species, accounted for less than 5% of the total time devoted to foraging activities (Supplementary Material Table 3). The average time spent per diving event (mean ± standard deviation) was estimated at 5.12 ± 0.85 s, 5.11 ± 1.09 s, and 4.87 ± 1.11 s for Red-gartered Coots, Red-fronted Coots, and White-winged Coots, respectively.

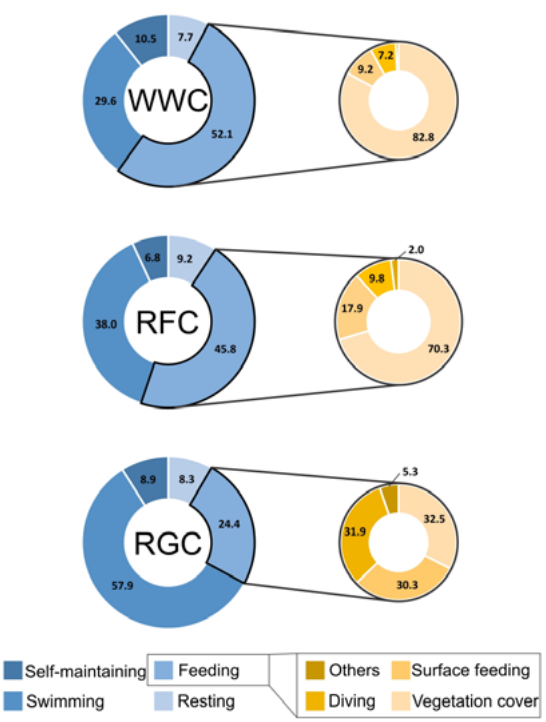


**Figure 2.** Percentage of time spent by the White-winged Coot (*Fulica leucoptera*, WWC), Red-fronted Coot (*F. rufifrons*, RFC), and Red-gartered Coot (*F. armillata*, RGC) in the main daily activity categories, and percentage of time spent (out of total feeding time) using the different feeding techniques, for the entire study period (i.e., August to November 2022) and combined time periods (i.e., morning, midday, and afternoon). The category 'Others' includes the feeding techniques 'head-neck submerged' and 'up-ending'. The percentage of time spent in the behaviors 'Agonistic interaction', 'Foot-paddling', and 'Flying' is not shown in the figure (together < 0.5% for each coot species).

Considering that the Overlap Index ranges between zero and one, high values (close to one) are interpreted as strong similarity in the mean time invested among the behaviors evaluated. The evaluation of the level of overlap for each activity among species, for the entire study period, showed very low and even null values for activities related to self-maintenance, swimming, feeding, and agonistic interactions (Fig. 3, Table 1). In contrast, for resting activities, this index yielded intermediate and low overlap values between White-winged and Red-gartered Coots and between Red-fronted and Red-gartered Coots, respectively (Fig. 3, Table 1). The analysis of the different feeding techniques used by these species throughout the study period showed low and null overlap values for almost all feeding techniques considered, except for food acquisition through head–neck submergence, where high values of the Overlap Index were observed between Red-fronted and Red-gartered Coots (Fig. 4, Table 1).

### Intra-daily activity budgets

The mean distribution of time allocated among

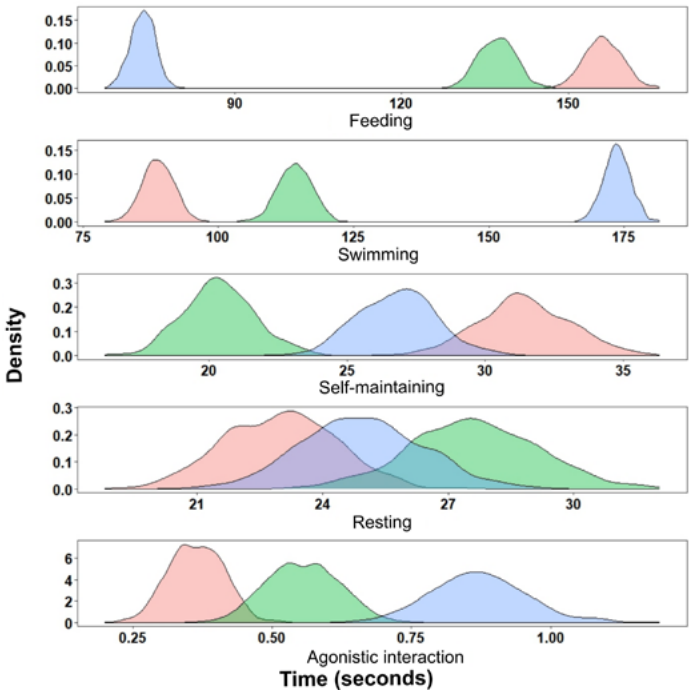


**Figure 3.** Distribution of the means of each daily activity category for the White-winged Coot (*Fulica leucoptera*, red), Red-fronted Coot (*F. rufifrons*, green), and Red-gartered Coot (*F. armillata*, blue), calculated from 1000 simulations for the entire study period (i.e., August to November 2022) and combined time periods (i.e., morning, midday, and afternoon). The *y*-axis represents the estimated kernel density of the distribution of the means for each behavior. The *x*-axis represents time, in seconds, allocated to each behavior.

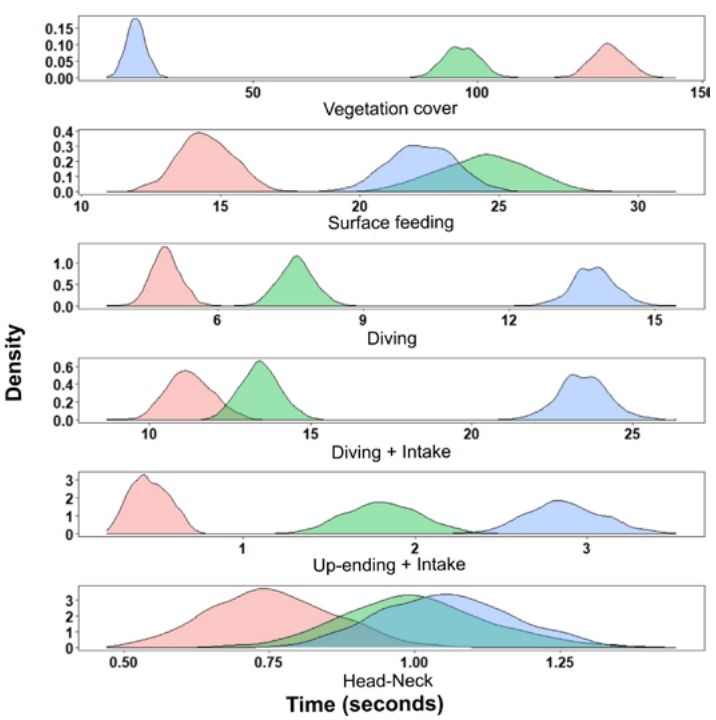


**Figure 4.** Distribution of the means of each feeding technique for the White-winged Coot (*Fulica leucoptera*, red), Red-fronted Coot (*F. rufifrons*, green), and Red-gartered Coot (*F. armillata*, blue), calculated from 1000 simulations for the entire study period (i.e., August to November 2022) and combined time periods (i.e., morning, midday, and afternoon). The *y*-axis represents the estimated kernel density of the distribution of the means for each behavior. The *x*-axis represents time, in seconds, allocated to each behavior. 'Vegetation cover': Feeding in areas outside the water column. 'Surface': Feeding at the surface of the water column. 'Diving + Intake' or 'Up-ending + Intake': Represents the sum of the time spent on the food acquisition technique plus the time spent ingesting the obtained food.

activity categories for each time period differed among the species studied (Supplementary Material Figs. 1–6). In general terms, Overlap Index values were low or null for most activities considered (Supplementary Material Tables 4–6), reflecting, for each species, differential time investment in each activity among time periods. White-winged Coots invested, similarly during the morning and midday periods, a greater proportion of their time in feeding activities, followed by activities related to searching (i.e., swimming; Supplementary Material Fig. 1, Tables 2 & 4); both activities had similar time investment for this species during the afternoon period (Supplementary Material Table 2). Although to a lesser extent, activities related to resting were mostly represented, similarly, during midday and afternoon periods, whereas White-winged Coots invested more time in self-maintenance activities during the afternoon period (Supplementary Material Fig. 1, Tables 2 & 4). Red-fronted Coots invested more time in feeding activities during morning hours, followed by swimming, whereas during midday and afternoon periods the time devoted to both behaviors was similar (Supplementary Material Fig. 3, Tables 2 & 5). For this species, resting was the third activity accumulating the most time during midday and afternoon periods, followed by preening, which was similar, in terms of time invested, to resting during morning hours (Supplementary Material Fig. 3, Tables 2 & 5). Regarding Red-gartered Coots, activities related to food searching dominated the proportion of time invested by the species across the three time periods, being higher during the morning (Supplementary Material Fig. 5, Tables 2 & 6), followed by feeding, which showed its highest values during the midday period. Resting activities for this species were higher during midday and self-maintenance was highest during the afternoon (Supplementary Material Fig. 5, Tables 2 & 6).

Regarding the different feeding techniques, those performed outside the water body (i.e., in surface vegetation) largely dominated the time budget invested across the three time periods for both White-winged and Red-fronted Coots, being higher in both cases during morning hours (Table 1; Supplementary Material Figs. 2 & 4, Tables 2 & 3). In the case of Red-gartered Coots, surface feeding and feeding outside the water body dominated feeding time during the afternoon and midday periods, respectively, whereas

**Table 1.** Overlap Index between the empirical distributions of the means of each activity category and feeding techniques among the study species, calculated from 1000 simulations, for the entire study period (i.e., August to November 2022) and combined time periods (i.e., morning, midday, and afternoon). 'Vegetation cover': Feeding in areas outside the water column. 'Surface': Feeding at the surface of the water column. 'Diving + Intake' or 'Up-ending + Intake': Represents the sum of the time spent on the food acquisition technique plus the time spent ingesting the obtained food.

| | **White-winged Coot – Red-fronted Coot** | **White-winged Coot – Red-gartered Coot** | **Red-fronted Coot – Red-gartered Coot** |
|---|---|---|---|
| **Activity** | | | |
| Feeding | 0.01 | 0.00 | 0.00 |
| Swimming | 0.00 | 0.00 | 0.00 |
| Self-maintenance | 0.00 | 0.14 | 0.02 |
| Resting | 0.12 | 0.51 | 0.39 |
| Foot-paddling | 0.68 | 0.14 | 0.11 |
| Flight | 0.62 | 0.53 | 0.39 |
| Agonistic interaction | 0.10 | 0.00 | 0.04 |
| **Feeding technique** | | | |
| Vegetation cover | 0.00 | 0.00 | 0.00 |
| Surface | 0.00 | 0.00 | 0.43 |
| Diving | 0.00 | 0.00 | 0.00 |
| Diving + Intake | 0.11 | 0.00 | 0.00 |
| Up-ending | 0.00 | 0.00 | 0.00 |
| Up-ending + Intake | 0.00 | 0.00 | 0.02 |
| Head-neck submerged | 0.31 | 0.20 | 0.82 |

during morning hours feeding outside the water body as well as diving techniques accounted for the greatest amount of time (Supplementary Material Fig. 6, Tables 3 & 6).

## DISCUSSION

The present study is the first to address the time invested in daily activities by three coot species occurring in sympatry in highly anthropized coastal wetlands in southeastern Buenos Aires Province. The protocol implemented in this study does not rely on an inferential statistical model but rather follows an exploratory and descriptive approach. Therefore, its results and comparisons with other studies discussed in this section should be interpreted with caution. On the other hand, for a better interpretation of the results obtained, it is important to note that although the sampling period of the present study (i.e., August–November) coincides with the breeding period of these species in other regions of the country (De la Peña 2025), we did not observe individuals exhibiting behaviors related to reproduction (e.g., courtship, copulation, egg laying), nor did we record eggs or chicks. This apparent absence of reproductive activity represents a limitation when comparing and generalizing the results. For this reason, and because time investment in different behaviors is affected by the stage of the breeding period, in the present section we have compared our results with other studies conducted during both the breeding and non-breeding periods. In addition, we have considered other scenarios such as the presence of non-breeding individuals. Among the possible scenarios that could explain the results obtained here, it is possible that birds reproduced before or after the sampling period, or even at other sites not surveyed (e.g., Reserva Natural del Puerto Mar del Plata). Another possible explanation is that during 2022 (the year of data collection) adverse climatic events may have occurred that affected reproduction. However, we do not rule out the possibility that some of these species may have been breeding during the evaluated period, given that in other years coot chicks have been observed in the lagoons studied (JPSP, MPB, pers. obs.). We also do not rule out the possibility that individuals present in these lagoons were juveniles or non-breeders. In Buenos Aires Province, the reproductive biology of these species has not yet been studied, and such studies are scarce even at the regional level (see Salvador 2012, Echevarria et al. 2022). Although in other parts of Argentina the breeding period of the species studied occurs between August and April, peak egg laying has been identified during December and January (Salvador 2012, Echevarria et al. 2022). The possibility that the populations of the three coot species using the study area during the evaluated period consisted of juveniles and/or non-breeding individuals should be considered when comparing our results with other studies at both regional and global scales.

In the study area, during the months of August to November, the three coot species studied invested the greatest proportion of their time in activities related to searching for and obtaining food. For White-winged and Red-fronted Coots, our results are consistent with those reported during the breeding period for other coot species inhabiting the Northern Hemisphere (i.e., North America; Ryan & Dinsmore 1979). Time budget studies conducted during the breeding period in the American Coot (*F. americana*) showed that this species invests from 50–70% of its time in feeding activities, while activities related to resting and self-maintenance ranged from 6–10% and 8–15%, respectively (Ryan & Dinsmore 1979). On the other hand, studies conducted on the Eurasian Coot (*F. atra*) during the non-breeding period in other regions (i.e., Algeria, Belgium, Ireland, India) showed diverse and contrasting values of time investment (Draulans & Vanherck 1987, Irwin & O'Halloran 1997, Baaziz & Samraoui 2008, Ryma & Mouloud 2018, Mukherjee et al. 2023). Baaziz & Samraoui (2008) and Ryma & Mouloud (2018) observed that the Eurasian Coot invested 75–80% of its time feeding, 15% in activities related to food searching, and less than 5% combined in resting and self-maintenance activities. For this species, Draulans & Vanherck (1987) reported that feeding and food searching accounted for approximately 55% and 30% of the time invested throughout the day, respectively, while self-maintenance accounted for around 11%, and no resting activities were observed. Irwin & O'Halloran (1997) determined that the Eurasian Coot invested similar amounts of time swimming and feeding, at 38% and 36%, respectively, and approximately 7% and 5% in resting and self-maintenance activities, respectively. Mukherjee et al. (2023), on the other hand, recorded food searching as the main activity at approximately 40%, followed by resting at 30%, and third, feeding activities at around 18%. Variation among regions in time budgets for the Eurasian Coot was mainly attributed to variability in trophic resource diversity and availability, and to environmental variability (Draulans & Vanherck 1987, Irwin & O'Halloran 1997, Ryma & Mouloud 2018). In our study, the Red-gartered Coot showed time budgets that differed from the other species evaluated, mainly in relation to

feeding activities, with only the time invested in food searching being similar to that recorded during the non-breeding period for the Eurasian Coot (Mukherjee et al. 2023). Regarding agonistic interactions and other behaviors such as flying, our results are consistent with those previously reported (< 1%; Ryan & Dinsmore 1979, Draulans & Vanherck 1987, Irwin & O'Halloran 1997, Ryma & Mouloud 2018, Mukherjee et al. 2023).

With respect to the feeding techniques observed, the results obtained in this study differed from those reported for these and other coot species. Our results indicate that White-winged and Red-fronted Coots select areas outside the water body to feed, especially during morning hours. In contrast, Red-gartered Coots invested a greater proportion of their time obtaining food within the water body, both at the surface and through diving techniques. Although coots include a wide diversity of seeds and arthropods in their trophic spectrum, feeding mainly on vegetation at the water surface has been recognized by other authors as the main feeding mechanism in these birds (Draulans & Vanherck 1987, Irwin & O'Halloran 1997, Baaziz & Samraoui 2008, Olguín et al. 2013, Ryma & Mouloud 2018). However, a single study reported diving as the technique accounting for the greatest amount of feeding time in the Eurasian Coot, followed by feeding at the water surface (Mukherjee et al. 2023). The proportion of time invested in other feeding techniques by the coots analyzed in our study, such as those in which individuals submerge the head, neck, or part of the body, fell within the ranges reported in other studies focused on coots (Draulans & Vanherck 1987, Irwin & O'Halloran 1997, Mukherjee et al. 2023). Regarding diving times, the three coot species evaluated invested a similar amount of time (~ 5 s) in each diving event. These results differ from those reported for other species such as the American Coot, whose average times ranged from 2–3 s (Batulis & Bongiorno 1972). In the case of the Red-gartered Coot, diving time was shorter than previously reported for the species in the region (~ 8.5 s). It should be considered that previous reports involved individuals feeding on crabs (García et al. 2008), whereas in the present study individuals fed on vegetation. In waterbirds such as coots, water depth and the diversity and abundance of submerged vegetation are some of the factors that determine dive duration (Batulis & Bongiorno 1972).

It has been shown that increased human activity in coastal environments negatively affects the richness and abundance of coots and other waterbirds, and it also generates avoidance behavior or displacement away from shoreline areas, which are in turn subject to greater anthropogenic pressure (Cardoni et al. 2008, Chávez-Villavicencio et al. 2015). Several authors have highlighted the importance of these behavioral changes, suggesting that individuals that are more alert to potential predators or threats may invest less time in feeding and resting activities, which may directly affect reproductive success (Beale & Monaghan 2004, Cardoni et al. 2008, Borgmann 2011). In our study, we characterized time budgets invested in daily activities in three coot species under natural conditions. However, these were recorded during weekdays, when visitor presence is lower. Likewise, the study period, which extended until December, did not include the summer months, when visitor numbers increase considerably due to the use not only of the Punta Mogotes beach resort complex but also the surrounding green spaces around all the lagoons in the complex (Bouvet et al. 2005, De Marco et al. 2005, Richeri 2011). For this reason, our study did not include comparisons of behavioral changes resulting from external stressors such as visitor presence and/or tourist activities. We consider it important to develop studies that allow for a better understanding of this issue in the study area, given that, due to its intrinsic characteristics, port, industrial, commercial, and tourism activities predominate in the surrounding area, with the potential to impact the avifauna present, as well as other local fauna (De Marco et al. 2005).

On the other hand, future studies should aim to obtain information on the physical characteristics of the study area, such as depth, as well as the vegetation present. This information would allow a better understanding of trophic behavior, dive times, energetic return (Batulis & Bongiorno 1972), as well as differential use of sectors of the water bodies (Heimsath et al. 1993). It should be noted that vegetation present in water bodies such as the lagoons evaluated is not only used as a food resource by a wide diversity of birds, but also functions as shelter (Traut & Hostetler 2003, Murray et al. 2013, Alikhani et al. 2021), where individuals can protect themselves from threats present in the area, such as unsupervised dogs (Berón & Seco Pon 2024) and feral dogs, some of which were observed entering the water with the intention of capturing birds (MH, pers. obs.). Given that the behaviors exhibited by an individual may be affected by the presence of other individuals both at the conspecific and heterospecific levels (Yasué 2005, Gil et al. 2018, Mukherjee et al. 2023), it would be relevant for future studies to evaluate the effect of group size as well as

assemblage composition.

Finally, it is essential to know and understand basic aspects of the biology of waterbird species that use these urban ecosystems, as they are exposed to various anthropogenic impacts. For this purpose, baseline behavioral studies play a fundamental role in understanding the spatial and temporal use that waterbirds make of these urban lagoons. This will make it possible to recommend potential management measures to ensure the conservation of the avifauna using the area, considering that it is not only part of a relic of coastal wetlands, but is also designated as a locally protected area and is adjacent to the Reserva Natural del Puerto Mar del Plata and an Important Bird Area (IBA BA12; Di Giacomo et al. 2007).

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## SUPPLEMENTARY MATERIAL

You can access the supplementary material for this article by visiting the link: https://doi.org/10.56178/eh.v41i1.1534.

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# NEST CHARACTERISTICS OF SECONDARY CAVITY-NESTING BIRDS USING NEST BOXES IN LOWER PARANÁ DELTA PLANTATIONS

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**ABSTRACT:** The Lower Paraná Delta landscape has been heavily modified by forestry and livestock production, resulting in the transformation of original environments and changes in resource availability for bird communities. Insectivorous cavity-nesting birds are potential providers of biological pest control in productive systems, which is why the use of nest boxes has been proposed as a sustainable forest management tool and as an opportunity to study the reproductive biology of poorly known species. In this study, we characterized nests built in nest boxes by the Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), Swainson's Flycatcher (*Myiarchus swainsoni*), Streaked Flycatcher (*Myiodynastes maculatus*), Greyish Baywing (*Agelaioides badius*), and Southern House Wren (*Troglodytes musculus*) in a forest landscape dominated by Salicaceae plantations in the Lower Paraná Delta, Buenos Aires, Argentina. Fifty nests from the 2020–2025 breeding seasons were analysed. Nests of the Swainson's Flycatcher were characterized by a predominance of soft materials (moss, plant fibers, hair, and feathers) and artificial material. Nests of the Greyish Baywing were mainly composed of plant fibers, while Southern House Wren nests consisted primarily of branches. Nests of the Streaked Flycatcher and the Narrow-billed Woodcreeper were composed of a single material: petioles and bark, respectively. All the aforementioned species built nests with a defined cup and species-specific morphometric parameters, except for the Narrow-billed Woodcreeper, whose nests lacked a defined structure. This study provides the first characterization of nests built in nest boxes by these species in the Lower Paraná Delta, including previously unpublished information on their reproductive biology.

**KEYWORDS:** *nest box, nest composition, nest morphometry, Paraná Delta, Salicaceae plantations*

Secondary cavity-using birds, in this case nesters, are those that use preexisting cavities, whether natural or excavated by other species. Thus, the availability and quality of these shelters condition their local survival (Cockle et al. 2011a, 2011b, Van der Hoek et al. 2017). Many of these birds are insectivorous and could play a fundamental role in insect control and the ecological balance of various ecosystems, particularly forested ones (Monteagudo et al. 2023). The replacement of native forests by commercial plantations with exotic species tends to reduce the availability of cavities (Politi et al. 2009), which has driven the increasing use of nest boxes as a management strategy to mitigate this loss (Cockle et al. 2011a, Olah et al. 2014). The effectiveness of this measure in increasing reproductive success does not depend solely on the availability of nest boxes, but also on the availability of suitable building materials. Changes in vegetation can affect these materials and, consequently, nest structure and chick survival (Álvarez &

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Barba 2009, Honorato et al. 2016). Nest composition is a good indicator of habitat use and quality during the breeding period, and fulfills key functions such as thermal insulation, support, and protection (Martínez Vilalta et al. 2002, Calvelo et al. 2006, Mainwaring et al. 2014). In turn, the position of the nest within the cavity also modulates these factors (Bulit & Massoni 2004). Despite the importance of these variables, in the Neotropical region there is little detailed information on how secondary cavity-nesting birds build their nests (Bonaparte et al. 2024).

In Argentina, the available information on these species has focused on characterizing eggs, chicks, and aspects of reproductive behavior, such as parental care, clutch size, and chick development (Di Giacomo & Lanús 1998, Salvador 2014, De la Peña 2019, Jauregui et al. 2019). Nests in cavities are usually described through *in situ* observations, and although in some cases the main materials and measurements such as cup size and depth are recorded, obtaining this type of data is limited due to the difficulty of accessing cavities.

The Paraná Delta is an extensive wetland system that harbors a high diversity of birds, including resident and migratory species, some of them with some degree of threat (Quintana & Bó 2011, Fracassi et al. 2021). In the Buenos Aires sector of the Lower Delta, the landscape has undergone marked transformation in recent decades, mainly due to the expansion of plantations of salicaceous species (willows – *Salix* sp. and poplars – *Populus* sp.) that have replaced natural environments such as riparian forests and grasslands (Fracassi et al. 2021). The riparian forests of the Lower Parana Delta is dominated by characteristic tree species such as *Ocotea acutifolia*, *Nectandra falcifolia*, *Citharexylum montevidense*, *Inga vera* and *Erythrina crista-galli*, but is also composed of shrubs, vines, epiphytes, and herbaceous plants that currently exists in the form of relictual patches (Burkart 1957, Kalesnik et al. 2008). These changes in vegetation structure and composition could affect the availability of cavities for nesting, as well as the supply of materials that birds can use to build their nests, which could impact their reproduction and persistence in these productive environments (Atienzar Navarro et al. 2010).

With the aim of understanding nesting requirements and providing relevant information for management and conservation in productive forest environments, this study characterized the structure and composition of nests built in nest boxes, and described general aspects of the reproductive biology of five bird species: Streaked Flycatcher (*Myiodynastes maculatus*), Southern House Wren (*Troglodytes musculus*), Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), Swainson's Flycatcher (*Myiarchus swainsoni*) and Greyish Baywing(*Agelaioides badius*), in productive and natural forest environments of the Lower Delta of Buenos Aires.

## METHODS

### Study area

We conducted this study on the island sector of Campana and San Fernando (34°04'S, 58°53'W), Buenos Aires province, Argentina, within the Paraná Delta and Islands ecoregion (Burkart et al. 1999), covering an approximate area of 58,000 ha (Borodowski & Suárez 2005). It is a deltaic plain influenced by fluvial dynamics, which shapes the insular landscape (Summerfield 1991). Currently, it presents a mosaic of islands crossed by artificial channels, where livestock production and forestry of salicaceous species are mainly developed under embankment systems (Kandus et al. 2003). The climate is temperate and subhumid, with mean annual temperatures of 16.7°C to 18°C, annual precipitation of 1000 mm, and relative humidity of 79% (Arana et al. 2021).

Typically, the islands have a basin-like shape, with lowlands (80% of the surface) and levees (20%; Borodowski 2017). The lowlands, formerly occupied by tall grasslands of *Scirpus giganteus*, were transformed into exotic pastures for livestock and areas destined for poplar and willow plantations (Kandus 1997, Kandus et al. 2003, Biondini & Kandus 2006). The levees and mid-slopes, previously dominated by the riparian forests ecosystem—gallery forest and *Erythrina crista-galli* stands—were transformed into poplar plantations and secondary forest (Kalesnik & Quintana 2005).

The environments of the Lower Delta are strongly influenced by the implementation of land systematization works (i.e., ditches, embankments, and semi-closed systems) that allow drainage and flood control to adapt the land for forestry production (Borodowski & Suárez 2005). This change occurred due to practices of traditional silvicultural practices associated with the forest species, such as weeding, pruning, and thinning (Fracassi et al. 2021). In general, poplar plantations present low tree density, little stratification, and an understory dominated by herbaceous plants, mainly *Carex chilensis*. In contrast, willow plantations form denser environments, with two to three shrub strata dominated by exotic species such as American Pokeweed (*Phytolacca americana*) and

Blackberry (*Rubus ulmifolius*; Fracassi et al. 2021). Likewise, patches of secondary forest are recorded within plantations, resulting from the abandonment of productive areas, where original riparian species (*Myrsine laetevirens*, *Nectandra angustifolia*; *Erythrina crista-galli*) coexist with invasive species such as Yellow Iris (*Iris pseudacorus*) and Privet (*Ligustrum* sp.), forming a heterogeneous mosaic of habitats in the forested landscape (Rossi & De Magistris 2014).

### Experimental design

The nests analyzed in this study came from a long-term research project developed by researchers from INTA Delta del Paraná, in which the contribution of insectivorous birds to the control of pest insects in forest systems and the use of nest boxes as a management tool are evaluated. Within that project, nest boxes made of poplar wood (2 cm thick) were designed, mailbox-type, measuring 30 × 15 × 15 cm (height × width × length) and with entrance holes of 4.5, 5, 6, and 7 cm in diameter, in order to attract five species of secondary cavity-using insectivorous birds (hereafter, focal species) present in plantations of the Lower Paraná Delta (Fracassi et al. 2021). The dimensions and characteristics of the boxes were defined according to body size and nesting preferences of these species. Among them, the range of entrance diameters sought to cover a potential range for the five focal species, adapting models previously used by these or other ecologically similar species (Proyecto VOLCAM 2007, Llambías & Fernández 2009, Calderón Martínez 2018). The nest boxes were installed in poplar and willow plantations and patches of secondary forest, at 25 m between each other and two meters above the ground, matching the vertical nesting range of the five focal species (De la Peña 2006), oriented northward and attached to tree trunks with wire. The boxes remained active for five consecutive breeding seasons (spring–summer 2020 to 2025), during which they were checked weekly. Identification of nesting species was carried out through direct observation of adults and recognition of nests, eggs, and chicks, with the support of specialized guides (De la Peña 2006).

During the development of this study, at the end of each breeding season (March–April), we recorded morphometric variables of the nest *in situ* (nest height, cup diameter, and depth) and collected the nests in paper bags for subsequent laboratory processing, where we evaluated their composition. We obtained the position of the cup relative to the entrance of the box and the percentage of cup/nest volume from photographs of the interior of the boxes taken during the breeding season, which allowed us to document nest structure and fresh materials before the appearance of chicks. In addition, these images made it possible to obtain variables related to reproductive aspects of the different species, such as clutch size, incubation duration, and chick development time until fledging. Entrance diameters of five and six cm were the most represented among the nests analyzed and were used by all focal species, although this distribution reflects only the nests that could be collected.

### Species characterization

For this study, we obtained nests from the five focal species: Streaked Flycatcher, Southern House Wren, Narrow-billed Woodcreeper, Swainson's Flycatcher, and Greyish Baywing. All these species use natural cavities, abandoned nests of woodpeckers (*Colaptes* sp.) or Rufous Hornero (*Furnarius rufus*), or artificial structures for nesting (Salvador 2014, Salvador & Narosky 2025), and are included in the insectivorous niche, although some incorporate seeds and/or fruits into their diet (Kirwan et al. 2022). Their local breeding period is concentrated between October and March. Among the mentioned species, Swainson's Flycatcher and the Streaked Flycatcher are migratory, being present in the region during the breeding season, while the rest are resident (Narosky & Yzurieta 2010, López-Lanús 2020). Clutch size varies between two and six eggs, and in all species both parents participate in the care and feeding of the chicks until they become fledgings (Salvador 2014, De la Peña 2019).

### Nest selection and analysis

We analyzed nests corresponding to the breeding seasons between 2020–2021 and 2024–2025. Whenever possible, we considered 'non-stacked' nests; that is, those not located below or above nests of other species in the same box, except in exceptional cases in which their morphology or composition remained intact. We based the analysis and morphometric and compositional characterization of nests on methodologies adapted from Bulit & Massoni (2004), Atienzar Navarro et al. (2010), and Honorato et al. (2016).

*Morphometric analysis*. For this analysis we considered a set of quantitative measurements describing the shape, dimensions, and physical structure of each nest. These metrics allow characterization of nest architecture associated with the construction strategy of each species. Given that all focal species (except the Narrow-billed Woodcreeper) present a

cup-shaped nest, we recorded: (a) cup diameter and depth (Supplementary Material, Fig. 1a) and (b) nest height. We measured the three variables *in situ*, in centimeters and with a millimeter ruler, inside the nest box and prior to nest collection, to avoid biases derived from deformation of the material during extraction and storage. We estimated other variables visually, based on images taken from inside the nest boxes during monitoring in the breeding season: (1) cup location (anterior, central, or posterior) relative to the entrance cavity of the nest box (Supplementary Material, Fig. 1b) and (2) percentage volume of the cup relative to the nest (Supplementary Material, Fig. 1c).

*Compositional analysis*. In the laboratory we disassembled each nest and classified its materials by type: 1. hair, 2. feathers, 3. bark, 4. petioles/fine branches (Ø < 2 mm), 5. thick branches (Ø > 2 mm), 6. leaves, 7. inflorescences, 8. grasses/reeds, 9. moss, 10. artificial material, 11. roots, and 12. 'other plant structures', recording the percentage volume of each, estimated visually after disaggregating each nest. Material identification was carried out through consultation with experts in botany and plant breeding at EEA INTA Delta, complemented with specific keys for *Salix* sp. and *Populus* sp. (Zuloaga & Belgrano 2017, Monteoliva 2024) and with regional flora guides of the Lower Paraná Delta and associated riparian areas (Rossi & De Magistris 2014, Rodriguez et al. 2018).

### Data analysis

For each species, we calculated the mean percentage value and standard deviation (SD) of the volume of each material item used in nest construction, as well as of the morphometric variables analyzed, based on the set of nests selected during the 2020–2025 breeding seasons.

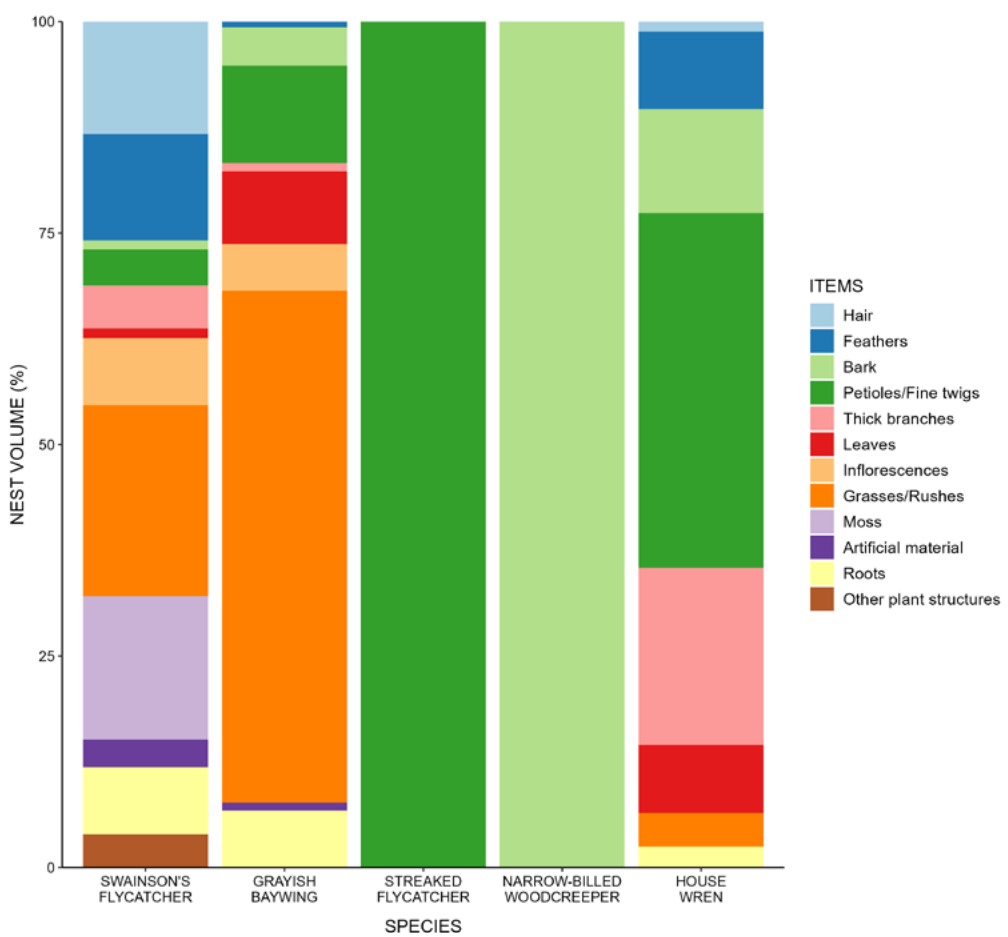


**Figure 1.** Mean percentage volume of the materials used for nest construction of Swainson's Flycatcher (*Myiarchus swainsoni*), Greyish Baywing (*Agelaioides badius*), Streaked Flycatcher (*Myiodynastes maculatus*), Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), and Southern House Wren (*Troglodytes musculus*), in nest boxes located in a forest matrix in the Lower Paraná Delta, Buenos Aires, Argentina, during five consecutive breeding seasons (2020–2025).

## RESULTS

We analyzed 50 nests from the five focal species: 44 for structure and composition and six for composition only (four nests of the Narrow-billed Woodcreeper without defined structure, and two flattened nests). From the Southern House Wren and Swainson's Flycatcher, we collected nests in poplar plantations, willow plantations, and secondary forest (House Wren: $n$ = 5, 5 and 7; Swainson's Flycatcher: $n$ = 5, 5 and 2). In the case of the Greyish Baywing and the Streaked Flycatcher, we collected nests in poplar and willow plantations (Greyish Baywing: $n$ = 5 and 5; Streaked Flycatcher: $n$ = 5 and 2), which were the only environments with nesting records. Finally, for the Narrow-billed Woodcreeper we collected nests in willow plantations ($n$ = 4), which was the only environment where it was nested. In general, nests presented a defined cup (except in the Narrow-billed Woodcreeper) and varied in volume and position within the box, with nest dimensions characteristic of each species (Table 1).

The incubation period ranged between 13 and 16 days (minimum in Swainson's Flycatcher, maximum in Streaked Flycatcher), while chick duration in the nest ranged between 14 and 17 days (minimum in the Southern House Wren, maximum in Streaked Flycatcher), and clutch size was larger in Swainson's Flycatcher, Greyish Baywing, and Southern House Wren (~ 4–5 eggs) than in Streaked Flycatcher and Narrow-billed Woodcreeper (~ 2–3 eggs; Table 2).

Nests were built mainly with plant materials, with a lower contribution of animal and artificial materials. In multiple species we found a predominant use of material from plantation salicaceous species (virtually 100% of the composition in nests of Streaked Flycatcher and Narrow-billed Woodcreeper, and 80% in Southern House Wren in plantations). The most frequent elements were branches and petioles, herbaceous fibers, and bark (exclusive material in Narrow-billed Woodcreeper), whereas moss, feathers, hair, and nylon were characteristic of Swainson's Flycatcher (Fig. 1).

**Table 1.** Mean values (± SD) of the morphometric variables analyzed in the nests of: Swainson's Flycatcher (*M. swainsoni*), Greyish Baywing (*A. badius*), Streaked Flycatcher (*M. maculatus*), and Southern House Wren (*T. musculus*), in nest boxes located in a forest matrix in the Lower Paraná Delta, Buenos Aires, Argentina, during five consecutive breeding seasons (2020–2025).

| | Swainson's Flycatcher | Greyish Baywing | Streaked Flycatcher | SouthernHouse Wren |
|---|---|---|---|---|
| Number of nests | 12 | 10 | 7 | 15 |
| Cup/nest volume (%) | 26.66 ± 5.36 | 45.00 ± 15.27 | 46.42 ± 11.70 | 34.33 ± 10.32 |
| Cup diameter (cm) | 6.28 ± 1.45 | 7.40 ± 2.22 | 8.14 ± 1.37 | 5.70 ± 0.80 |
| Cup depth (cm) | 1.97 ± 0.62 | 3.35 ± 1.81 | 2.15 ± 0.78 | 3.95 ± 1.36 |
| Nest height (cm) | 4.30 ± 1.72 | 7.33 ± 1.74 | 8.29 ± 2.70 | 7.86 ± 2.03 |
| Cup position within the nest | Back (11/12) | Center (7/10) | Back (6/7) | Variable |

**Table 2.** Reproductive variables recorded by species: incubation period (days), nestling period (days), clutch size, and number of chicks, calculated from images of the interior of nest boxes taken during the 2020–2025 breeding seasons, located in a forest matrix in the Lower Paraná Delta, Buenos Aires, Argentina.

| Species | Incubation (days) | Nestling period (days) | Number of eggs | Number of chicks |
|---|---|---|---|---|
| Swainson's Flycatcher | 13.88 ± 0.72 | 16.38 ± 0.72 | 4.75 ± 0.48 | 4.25 ± 0.63 |
| Greyish Baywing | 13.44 ± 0.34 | 14.89 ± 0.39 | 5.38 ± 0.46 | 4.63 ± 0.42 |
| Streaked Flycatcher | 15.94 ± 0.50 | 17.19 ± 0.67 | 3.75 ± 0.16 | 2.63 ± 0.42 |
| Narrow-billed Woodcreeper | 15.30 ± 0.49 | 15.60 ± 0.30 | 2.60 ± 0.66 | 2.20 ± 0.49 |
| Southern House Wren | 14.70 ± 0.58 | 14.70 ± 0.85 | 4.60 ± 0.24 | 4.20 ± 0.37 |

Below, we detail compositional characteristics by species.

### Swainson's Flycatcher

We recorded up to 12 material items forming a dense interwoven structure of diverse soft materials, with a predominance of wild plant materials; that is, not derived from planted salicaceous individuals, especially grasses and reeds (23%), moss (17%), and inflorescences (8%) corresponding to the silky fruit material (pappus) of the inflorescence of thistles of the genus *Cirsium* sp., and materials of animal origin (hair, 13% and feathers, 13%; Fig. 1). Plant fibers (grasses and reeds), moss, and hair were used to interweave the nest matrix, and feathers and part of the hair to line the cup and cover the eggs (Fig. 2A). The use of other materials was lower; bark (1%), roots (8%), fine branches (4%), coarse branches (5%), and notably artificial material (3%; Fig. 1). In the latter category we classified materials such as nylon, plastic bags, and adhesive tape, used in low volume, in 50% of cases to line the cup. In two nests, we found uncommon plant materials (classified as 'other plant structures'): pine needles in one case and an aquatic plant of the genus *Salvinia* sp. ('Acordeón'), placed whole as part of the nest matrix.

### Greyish Baywing

Nests showed a semi-dense to dense weave, with up to nine material items recorded (Fig. 1). Herbaceous fibers grouped under grasses and reeds were most common, representing on average 61% of the volume, including species such as reeds of the genus *Carex* sp., Pampas Grass (*Cortaderia selloana*), and other unidentified grasses. The finer material of this category, together with roots (7%), formed the cup (Fig. 2B). In lower proportion, fine branches (11.5%) and coarse branches (1%), leaves (9%), and inflorescences (5.5%) from plantation individuals were incorporated, forming the nest matrix. We also recorded nylon in one of the 10 analyzed nests, classified under 'artificial material'. It is worth noting that we observed a high frequency of nests built on top of those of other birds, mainly Southern House Wren (six of the 10 analyzed nests).

### Streaked Flycatcher

Nests consisted of a semi-dense to dense weave of a single material (100% of nest composition) classified as petioles/fine branches (Figs. 1 & 2C), which could be identified in all analyzed cases as belonging to poplars due to the presence of floral peduncles with cotton-like remains characteristic of their inflorescences.

### Narrow-billed Woodcreeper

The nest structure consisted exclusively of a layer of bark without forming a defined cup, therefore we did not record morphometric measurements. Eggs were laid on this layer, generally located in the center (Fig. 2D). In all cases, bark fragments retained characteristic features of the cultivated willow varieties where the species nested.

### Southern House Wren

We identified a total of eight material items in the nests (Fig. 1). The main material for nest construction was branches of varying thickness (fine with diameter < 2 mm and coarse with diameter > 2 mm; Fig. 2E), originating both from plantation species (poplars or willows) and from wild woody vegetation of species growing in the plantation understory (e.g., European Dewberry, *Rubus caesius*), or from species of secondary forest, depending on the environment where the nest was built. Branches, which represented on average 62.7% of nest volume, were arranged forming a

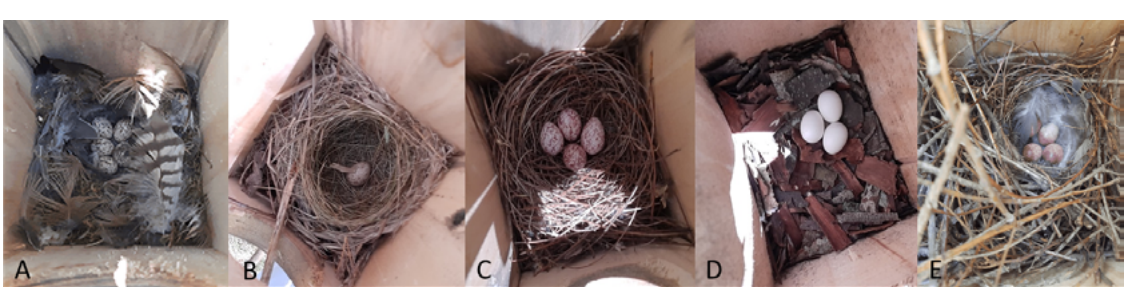


**Figure 2.** Image of the interior of the nest box with nest and eggs of A) Swainson's Flycatcher (*Myiarchus swainsoni*) in willow plantations, B) Greyish Baywing(*Agelaioides badius*) in willow, C) Streaked Flycatcher (*Myiodynastes maculatus*) in poplar plantations, D) Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*) in willow, and E) Southern House Wren (*Troglodytes musculus*) in willow. All images correspond to the 2021–2022 breeding season, in a forest matrix in the Lower Paraná Delta, Buenos Aires, Argentina.

structural matrix of crossed branches and delimiting the cup (Fig. 2E). The contribution of other materials was low: we recorded grasses (4%), bark (12%), and leaves (8%). Among the latter, the use of poplar leaf blades was common in nests from this type of plantation. We found feathers lining the cup or more generally incorporated into the nest matrix.

## DISCUSSION

This study constitutes the first comprehensive characterization of nests of five species of secondary cavity-nesting birds in nest boxes in the Lower Paraná Delta. In particular, we present the first detailed description of nest box nests of Swainson's Flycatcher and Greyish Baywing, substantially expanding the information previously available in Argentina.

Although information on the nest of Swainson's Flycatcher is scarce, the general structure was similar to that described in other studies (De la Peña 2019, Joseph 2020), and its composition to that observed in other members of the family Tyrannidae (Hansell 2000). The use of soft materials, that is, those that do not contribute to a rigid nest structure, such as moss, plant fibers, and feathers, has been suggested to be associated with thermal insulation, structural cohesion, and, in the case of moss, possible antimicrobial benefits (Clark & Mason 1985, Dubiec et al. 2013, Mainwaring et al. 2014). A novel finding was the incorporation of plastics and other artificial materials in cup lining, a practice common in urban birds (Reynolds et al. 2019), but not previously documented in this species. Although this behavior reveals flexibility in material selection, it is necessary to evaluate its potential impact on reproductive success. Multiple studies have reported negative effects on reproductive success associated with the use of artificial materials (Townsend & Barker 2014, Wang et al. 2021, Corrales-Moya et al. 2023). At the local level, research in the Pampas region has documented critical consequences such as open wounds, amputations, and mortality by strangulation, mainly associated with the use of polypropylene threads and fishing lines (Yassin et al. 2025). These findings are consistent with regional reports warning about risks of suffocation by plastics, alterations in nest thermoregulation, and increased predation due to the high visibility of artificial materials (Azevedo-Santos et al. 2022, Lindwedel Cruz 2023).

Most nest materials could be found in the understory of the collection environment. For example, nests collected in poplar stands under silvopastoral management showed a higher proportion of hair. This raises questions about the scale of resource search and the effect of local availability on nest quality, especially in forest systems where management reduces understory vegetation. In this sense, it is important to integrate future vegetation surveys with nest studies to evaluate how silvicultural management, particularly practices such as weeding, influences the availability of construction resources. On the other hand, we recorded a higher average clutch size (+ 2 eggs) compared to that reported in the existing literature, and a slightly shorter incubation period (- 2.12 days; De la Peña 2019).

Nests of the Greyish Baywing showed a construction pattern consistent with that described for nests in natural cavities: coarse materials forming the base and periphery of the cup, and fine and flexible materials in the interior (De la Peña 2019, Quiroga & Llugdar 2019). In this study, we recorded the predominance of herbaceous fibers (grasses) as the main nest material. We also observed a high frequency of nests built on structures previously constructed by other birds, mostly Southern House Wren. Although our study did not directly assess secondary parasitism, this pattern is consistent with behaviors previously documented for the Greyish Baywing (Luchesi & Astié 2017). On the other hand, the average clutch size documented in this study may be biased, as during the examination of field photographs we could not distinguish eggs of this species from those of the Screaming Cowbird (*Molothrus rufoaxillaris*), which parasitizes its nests (Lowther et al. 2020).

The composition of Streaked Flycatcher nests matched what has been reported for the species (Di Giacomo & Lanús 1998), although here a marked use of poplar petioles was recorded. In contrast to observations in natural cavities, we recorded smaller diameter and depth than those documented by other authors (e.g., Di Giacomo & Lanús 1998). However, as experimental studies have shown (Evans et al. 2002), structural characteristics of artificial cavities can modify certain nest attributes. This bias associated with the use of nest boxes is a general limitation for comparison with descriptions from natural cavities and should be considered when interpreting the results for all analyzed species (Bonaparte et al. 2024).

The composition of Narrow-billed Woodcreeper nests agrees with that reported by Pizo (2018) in Brazil and Jáuregui et al. (2019) in Argentina, who also recorded rudimentary bark nests, although other studies mention the use of leaves, herbs, or wood chips (Marantz et al. 2020). This study suggests an almost

exclusive preference for willow bark in Delta plantations. The absence of an elaborate structure indicates a simple construction strategy, likely associated with the reproductive biology of the species, in line with what has been reported for other members of the genus, such as the Scalloped Woodcreeper (*Lepidocolaptes falcinellus*; Bodrati & Cockle 2011). Regarding reproductive variables, we recorded a smaller clutch size (–1 egg) compared to average values reported in the current literature (De la Peña 2019).

The Southern House Wren is the species with the most information available in the literature (Atienzar Navarro et al. 2010, Honorato et al. 2016, Medrano et al. 2019) due to its wide distribution and adaptability, which allow it to occupy a vast variety of environments (Honorato et al. 2016, León 2024). The use of artificial structures, such as nest boxes, is a widely documented and consistent behavior across studies in this species (Muller et al. 1997, Alworth & Scheiber 2000, Vergara 2007, Llambías & Fernández 2009, Fernández et al. 2020). In this context, this work expands that knowledge by characterizing for the first time the material with which this species builds its nest and its general structure in salicaceous plantations of the Paraná Delta. In this context, it maintained a conserved construction pattern in the set of analyzed nests: accumulation of crossed branches as a structural matrix, complemented with leaves and feathers, varying the origin of these materials (plantation or wild) depending on the environment where the nest was collected, suggesting a strategy of exploiting local resources.

In all species we evaluated the position of the cup relative to the entrance of the nest box, a trait associated both with reducing predation risk (the main cause of failure in nest boxes; Llambías & Fernández 2009) and with regulating thermal conditions (Mainwaring et al. 2014, 2015b, Deeming & Mainwaring 2015). As we found no specific previous records for the species analyzed here, these results represent a novel contribution. Likewise, standardized recording of nest microarchitecture may be a key tool for future comparative studies (Mainwaring et al. 2023), allowing identification of adaptive patterns among species and evaluation of the influence of management and local conditions on their reproductive strategies.

## FINAL REMARKS

This work provides novel information on nest structure and composition in forest plantations, relevant for understanding reproductive biology in transformed landscapes and for designing management measures that favor the persistence of these birds and their potential ecosystem service of pest control.

Likewise, we provide a detailed description of the nests of *L. angustirostris*, *M. swainsoni*, *M. maculatus*, *A. badius*, and *T. musculus*, as valuable input for future studies. In general, although we recorded species-specific variations relative to what has been described for natural cavities, a construction pattern consistent with the identity of each species was maintained, suggesting some stability in nesting strategies despite the context of modified environments.

In forest plantations, some species depend on resources closely associated with the planted species (e.g., poplar petioles, willow bark), whereas others rely on materials from the understory, surrounding vegetation, associated fauna, or even artificial elements. This diversity in the origin of resources and in construction strategies, from simple and specialized designs to more flexible compositions, may influence the ability to persist in transformed landscapes (Collias & Collias 1984, Mainwaring et al. 2014, Honorato et al. 2016).

From a management perspective, these differences are relevant. More dependent species may have their reproduction limited by changes in the availability of specific resources, whereas more generalist species may persist in modified environments. Future comparisons between plantations and native forest will allow evaluation of the functional value of these strategies and contribute criteria for silvicultural practices that favor the availability of nesting resources.

Finally, although nest boxes allowed standardization of sampling and access to the internal structure of nests, their use has limitations (Zhang et al. 2023, Bonaparte et al. 2024). Box dimensions may modify nest volume and the amount and proportion of materials used (Deeming et al. 2019), as well as alter the internal microclimate relative to natural cavities, introducing potential biases (Sudyka et al. 2022, 2023). Added to these limitations is the small sample size, which restricts detection of intraspecific variation and generalization of results (Verma & Verma 2020). Together, these constraints indicate that some observed patterns may be influenced by box design and low statistical representativeness, and future studies should incorporate natural cavities, microclimatic measurements, and larger sample sizes.

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## SUPPLEMENTARY MATERIAL

You can access the supplementary material for this article by visiting the link: https://doi.org/10.56178/eh.v41i1.1535.

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# KEY MARINE AREAS DURING PENGUIN MIGRATION IN THE ARGENTINE SEA: CONTRIBUTIONS TO THEIR CONSERVATION KNOWLEDGE

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**ABSTRACT:** During migration, seabirds concentrate in key oceanic areas associated with high productivity. Magellanic Penguins (*Spheniscus magellanicus*) and Western Rockhopper Penguins (*Eudyptes chrysocome chrysocome*) spend most of the non-breeding season migrating in the Argentine Sea. Here, we compared the distances and phenology of migratory trips between both species breeding in nearby colonies (< 20 km apart in Puerto Deseado, Santa Cruz). In addition, we evaluated the association of these colonies and other Magellanic Penguin colonies with marine fronts during migration. Between 2017 and 2024, we analyzed 186 geolocators recovered from adult individuals of both species. Western Rockhopper Penguins traveled greater total distances and moved farther offshore than Magellanic Penguins, but the maximum distances reached were similar. Magellanic Penguins departed from and returned to the colony earlier than Western Rockhopper Penguins, exhibiting interspecific reproductive allochrony. The most frequently used front by both species was the El Rincón Front. In the case of Magellanic Penguins, the Río de la Plata Front appears to act as the eastern limit of migration for individuals from northern colonies (60% of the population evaluated), whereas the Patagonian Current Front is used by individuals from southern colonies (16%). Under thermal anomalies, Western Rockhopper Penguins also used the shelf-break front. These findings reveal spatial and temporal segregation in habitat use by these species and highlight the importance of key areas for their conservation, such as the waters of El Rincón and the Río de la Plata.

**KEYWORDS:** *Argentine Sea, marine fronts, migration, non-breeding season, penguins*

Penguins are mesopredators or apex predators and given their abundance and distribution, play key roles in the trophic webs of the Argentine Sea (Falabella et al. 2009, García-Borboroglu & Boersma 2013). Their breeding sites are generally easily accessible and this consequently allows assessments of their reproductive success, health, and year-round distribution at sea that can be used as environmental indicators of ocean conditions (Boersma 2008). Two penguin species primarily use the Argentine continental shelf: the Magellanic Penguin (MP, *Spheniscus magellanicus*) and the Western Rockhopper Penguin (WRP, *Eudyptes chrysocome chrysocome*; but see Baylis et al. 2015, Baylis et al. 2021). Both species spend much of their annual cycle at sea and are migratory species, but breed in terrestrial colonies. The MP forms colonies from Islote Lobos (40°47'S), at the northernmost point of its range, southward along the entire Argentine Patagonian mainland coast and the islands of Tierra del Fuego and the Malvinas Islands (Raya Rey et al.

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2014, Millones et al. 2021, García-Borboroglu et al. 2022). MP also breeds along the Chilean coast, from the southern tip northward to Isla Algarrobo (33°22'S, 71°40'W). The total population (Atlantic and Pacific) is estimated at 1.2–1.6 million pairs (Boersma et al. 2013) and is classified by the IUCN (International Union for Conservation of Nature) as 'Least Concern' (BirdLife International 2020a). The WRP breeds in several colonies in the Malvinas Islands, on Isla de los Estados, and on several other islands in southern Chile south of 51°S (Pütz et al. 2013). During the 1980s, a small colony was discovered on Isla Pingüino (47°54'S, 65°42'O), the northernmost point of its distribution (Frere et al. 1993). This species has a global population of 900,000 pairs (Pütz et al. 2013, Raya Rey et al. 2014, Gandini et al. 2017), and its conservation status is considered Vulnerable (BirdLife International 2020b). The WRP shares breeding areas with the MP, although they do not form mixed colonies (Boersma et al. 2013, Pütz et al. 2013).

Much research has focused on the trophic ecology and at-sea movements of these two penguin species during the breeding season, a period during which they are central-place foragers (Schiavini & Raya Rey 2004, Oehler et al. 2018, Ainley & Wilson 2023). However, the non-breeding period has been studied far less extensively (Stokes et al. 1998, Pütz et al. 2000, Pütz et al. 2007, Raya Rey et al. 2007). The non-breeding period is important because it is during this stage that individuals face the greatest risks from predation, disease, exhaustion, food shortages, and adverse weather conditions (Newton 2008), which can subsequently affect populations. More recently, the advent of new technologies that are less invasive for penguins, such as satellite devices (Clarke & Kerry 1994, Wilson et al. 2004, Wilson et al. 2015), together with decreasing costs, has led to new studies providing information from different colonies and covering complete penguin migrations (Yamamoto et al. 2019, Barrionuevo et al. 2020, Dodino et al. 2021, Barrionuevo et al. 2023, Green et al. 2023).

Southern Atlantic MPs migrate northward from their colonies (Stokes et al. 1998, Pütz et al. 2007, Yamamoto et al. 2019, Barrionuevo et al. 2020, Dodino et al. 2021, Barrionuevo et al. 2023, Rebstock & Boersma 2023). However, partial migration occurs in this species: in colonies located in the southern portion of its range, some individuals migrate whereas others remain near their breeding colonies (Barrionuevo & Frere 2024). The areas used during this dispersal depend on the colony studied, with individuals also segregating in the environmental and trophic niches they occupy (Barrionuevo et al. 2023), resulting in extensive use of the Argentine shelf during winter. In addition, there is sex-based segregation, with females migrating closer to the coast than males (Yamamoto et al. 2019, Barrionuevo et al. 2020, Rebstock & Boersma 2023). In contrast, WRP migration differs substantially depending on the breeding colony (Pütz et al. 2002, Pütz et al. 2006a, Raya Rey et al. 2007, Ratcliffe et al. 2014, Green et al. 2023, Barrionuevo et al. 2025). Penguins from the Isla de los Estados colony migrate southward and then westward toward the Pacific Ocean, occasionally entering the Southern Ocean (Green et al. 2023). In contrast, penguins from the Isla Pingüino colony migrate northward while remaining on the Argentine shelf (Barrionuevo et al. 2025). In the Malvinas Islands, individuals follow one or the other migratory pattern depending on the colony (Ratcliffe et al. 2014). No sex-based segregation in space use during migration (Thiebot et al. 2015) or during the pre-molt trip (Dodino et al. 2024) has been found in this species. Recently, the migration of individuals of both species breeding in Puerto Deseado, Santa Cruz, one of the sites where they coexist, was analyzed using geolocators and stable isotopes (Barrionuevo et al. 2025). The results showed that WRPs differ from MP in both isotopic and spatial niche use, with the former concentrating their migration more along the shelf break and in the El Rincón region, whereas MPs migrate off Peninsula Valdés and San Matías Gulf, using to a lesser extent the waters off Buenos Aires Province and the Río de la Plata. Nevertheless, both species occupy relatively similar environmental niches, although MP use shallower and warmer waters than WRP (8.6°C vs. 11°C, Barrionuevo et al. 2025).

During migration, penguins may use marine fronts as key areas. Key marine areas are regions of the ocean with exceptionally high biological productivity where the structure of marine fronts (contact zones between different water masses) generates predictable aggregations of prey (Alemany et al. 2009). In the Argentine Sea, these fronts act as biological 'magnets' that facilitate foraging by penguins, as well as other seabirds and marine megafauna, by concentrating nutrients and biomass at specific locations along the shelf break and continental shelf (Falabella et al. 2009, Piola et al. 2018). Indeed, marine fronts are selected by many species because of their environmental characteristics and the presence of high concentrations of key prey (e.g., small fish and pelagic crustaceans). The spatial coincidence between fronts and primary production is generally very high (e.g., Acha et al. 2004), but it gradually decreases as higher

trophic-level organisms are considered because, due to their larger size, greater locomotory capacity, and more complex behavior, they are more independent of their environment (Alemany et al. 2018). In addition, from a physical perspective, a front can be defined as a line connecting points of maximum horizontal gradient in a given variable (typically temperature or salinity). Although this definition is conceptually correct, it has limited relevance for ecological studies because organisms do not live along a line; rather, they occur and concentrate within a region of 'frontal influence'. Therefore, fronts may be highly important for species even when there is little overlap with the line that physically defines the front (Acha et al. 2024).

It is during the aquatic phase, such as migration, that penguins face the greatest anthropogenic risks. Although both MPs and WRPs are exposed on land to anthropogenic threats associated with global change—such as exposure to high temperatures or extreme rainfall during the breeding season, resulting in increased chick and even adult mortality (Boersma & Rebstock 2014, Holt & Boersma 2022, Lera et al. 2023)—when at sea, bycatch in fisheries is moderately important, particularly for MPs, with records of mortality in gillnet and trawl fisheries (Crawford et al. 2017). Although mortality rates reported in specific studies are relatively low and do not compare with those of other pelagic seabird species (Favero et al. 2011, Tamini et al. 2015), they could still be important considering the cumulative effects across the species' extensive distribution, where it overlaps with different types of fisheries (Crawford et al. 2017). Another anthropogenic threat to which penguins on the Argentine shelf are exposed is oil exploitation. This was a major cause of MP mortality during the 1980s and 1990s, with an estimated 40,000 penguins dying annually during that period (Gandini et al. 1994). However, oil-related mortality rates have now declined dramatically due to appropriate mitigation measures (see Wagner et al. 2023). During episodes of seismic surveying in the oceans, associated with the exploration and exploitation of new hydrocarbon resources, highly intense artificial sounds are produced, which have been shown to temporarily reduce the abundance of Magellanic Penguins in affected areas (Seco Pon et al. 2019). On the other hand, contamination through the ingestion of marine debris is very common in juvenile penguins stranded along the coast (Di Beneditto et al. 2017, Seco Pon et al. 2023). However, except in rare cases, it is not a direct cause of mortality (Neto et al. 2021). This issue has been infrequently reported in breeding adults. Microplastics have also been found in feces of penguins admitted to rehabilitation centers (Mendez-Sanhueza et al. 2023), and various tissues have been found contaminated with organochlorines and heavy metals (Baldassin et al. 2016, Quadri-Adrogué et al. 2022); however, the actual impact of these contaminants on individuals remains unknown. Currently, global changes in the oceans are considered a potentially major threat to these species (Trathan et al. 2015), but evaluating this hypothesis requires a deeper understanding of the issue. To date, evidence has only been found in Western Rockhopper Penguins, including alterations in migratory patterns associated with sea-surface temperature anomalies (Raya Rey et al. 2007, Barrionuevo et al. 2025) and records of high mortality during the pre-molt trip stage that could not be attributed to other causes such as disease outbreaks (Boersma 1987, Morgenthaler et al. 2018). Projections of oceanic changes, particularly those related to sea-surface temperature and sea-surface height, indicate a reduction in preferred habitat for WRPs using the Pacific Ocean, but an expansion of habitat for those using the Atlantic Ocean (Green et al. 2023). Therefore, studies on the species' plasticity and its ability to adapt to new environmental scenarios will be highly important for conservation efforts.

To improve our understanding of migration and identify key marine areas used by both species, we established the following specific objectives: 1) To compare the characteristics of migratory trips (e.g., distances traveled and reached, phenology, and travel direction) of individuals of both species breeding in Puerto Deseado, Santa Cruz. 2) To evaluate the use of marine fronts by these species during migration. Subsequently, in the Discussion, based on the results obtained, we address the potential risks posed by different anthropogenic activities during migratory trips in both species.

## METHODS

### Study Sites

For the migratory study of the WRP, we worked with individuals from Isla Pingüino (47°54'S, 65°42'W), located in Santa Cruz, Argentina. This island lies within the interjurisdictional park Marino Isla Pingüino and hosts a recently established Western Rockhopper Penguin colony totaling 1581 breeding pairs. This colony has been increasing at a rate of 7.7% since 1985 (Gandini et al. 2017) and is probably the result of immigration from colonies in the Malvinas Islands (Gandini et al. 2017, Lois et al. 2020). Magellanic Penguins also breed on this island

(10,169 breeding pairs; Millones et al. 2021).

For the migratory study of MPs, we used three colonies distributed across almost the entire latitudinal extent of the species' breeding range. Much of the information compiled on migration from these colonies can be found in Barrionuevo et al. (2023). The colonies were: a) Estancia San Lorenzo (42°05'S, 63°54'W), located in the northern part of the breeding range, with a population of 240,000 breeding pairs, making it the largest colony of the species. This colony increased its population by 92% since the 1990s (Garcia-Borboroglu et al. 2022). b) Isla Quiroga, located within the Deseado Estuary and forming part of the Ría Deseado Provincial Reserve, situated 20 km from Isla Pingüino. It hosts 1,348 pairs of Magellanic Penguins and is surrounded within a 10-km radius of nearly 25,000 pairs, constituting a stable population (Millones et al. 2021). c) Finally, Cabo Vírgenes, located at the southern end of the breeding range, is the third-largest colony with 127,000 breeding pairs and has shown a 42% increase over the last 30 years (Millones et al. 2021).

### Fieldwork

During the late breeding season or molting period (February to March), between 2017 and 2024, we deployed 186 geolocators: 159 MK4 and 27 MK3 units (geolocator weight: 1.80 g and 2.5 g, respectively; less than 0.1% of the animals' body mass; Lotek, UK) on adult MPs and WRPs to track them during migration. The different models vary in their precision, with the MK4 representing a newer generation. These devices are attached to the tarsus using cable ties covered with heat-shrink tubing to avoid harming the animals (Ratcliffe et al. 2014b) and can be deployed relatively quickly, requiring less than three minutes. The devices were recovered when penguins returned from migration (September/October for MPs and November for WRPs). In the Supplementary Material, Table 1 shows the number of devices analyzed for each year and colony. Recovery averaged approximately 78.03% across all study years. In this study, we used only data from the migratory trip, excluding the pre-molt trip (see Statistical Analyses for details on how this distinction was made).

Penguins were captured at their nests by the leg using a specially reinforced hook designed to avoid injury. Males have a slightly wider bill than females, which allows sex determination (Gandini et al. 1992).

### Statistical Analyses

To download geolocator data, we used the Bastrack software (BioTrack 2013), and analyses were conducted using the R package *TwGeos* (Lisovski et al. 2015) in R (R Development Core Team 2021). Geolocators do not record positions directly; instead, they record natural light intensity every minute, storing the highest value every 5 min. They also record the state of the device (wet/dry) and temperature after a continuous period of 25 min in the same state. Therefore, to estimate positions, we defined twilight events (sunrises/sunsets) using the threshold method. Specifically, we selected an arbitrary threshold of 1.5 light units for all individuals and, for each trip, selected calibration periods to estimate a sun elevation angle and the error distribution (Lisovski et al. 2020). We then calculated 1000 possible migratory trajectories by modifying twilight times according to the twilight error distribution, resulting in 1000 location estimates per twilight event that represented the expected spatial distribution of possible locations. Finally, we used the R package *SGAT* (Wotherspoon et al. 2016) and Bayesian Markov Chain Monte Carlo (MCMC) methods to refine movement trajectories by incorporating prior information on the expected twilight error distribution, a spatial mask delimiting land and sea areas, a sea-surface temperature mask for calibration with temperature records from the device, and a movement model. Additional details can be found in Lisovski et al. (2020) and Barrionuevo et al. (2023).

For the first objective, comparing migratory-trip characteristics between MPs and WRPs breeding at nearby sites, we used only data from Isla Quiroga and Isla Pingüino. These colonies are located close to one another (~20 km apart), making comparisons between species more appropriate. In addition, we used only years for which sufficient data were available for both species (2019, 2021, 2022, and 2024).

To define departure from and arrival at the colony, we used the wet/dry state of the device because penguins rarely leave the water once migration begins. Departure was defined as the day on which records remained continuously wet for more than six hours, allowing short dry-state events (30 min), whereas arrival was defined as the day on which records remained continuously dry for more than six hours, allowing short dry-state events (30 min). This information was used to estimate migratory-trip duration. When data from the pre-molt trip were available (during which penguins also remain in the water for

extended periods), this data was excluded.

To calculate trip characteristics, we used the R package *track2KBA* (Beal et al. 2021), considering only the most probable trip for each individual. For each individual, we calculated the maximum distance reached (from the colony to the farthest point in a straight line), total distance traveled, and angular direction (the angle between the farthest point and the colony location, using geographic north as 0°).

These variables were then used, one at a time, as response variables in linear models (package *nlme*, Pinheiro et al. 2023). Predictor variables included sex, species, study year, the two-way interactions between species and sex and between species and year, and the three-way interaction. A total of 64 models were generated using the dredge function in the *MuMin* package (Bartón 2023). Models were ranked according to the Akaike Information Criterion corrected for small sample sizes (AICc). Following a parsimony criterion, we considered all models with ΔAICc < 4 to be competitive. To obtain robust parameter estimates, we performed model averaging across this set of models. To evaluate whether a predictor was informative within this model set, we examined its 95% confidence intervals using the *confint* function. Predictor variables whose confidence intervals included zero were considered non-informative, whereas those excluding zero were considered important in explaining variation in the response variable (Grueber et al. 2011). For informative variables, post hoc multiple comparisons were performed using Estimated Marginal Means (EMMeans) with the *emmeans* package (Lenth 2024), using a significance level of $\alpha = 0.05$.

For the second objective, evaluating overlap between penguin-use areas and marine fronts, we determined the location of fronts present during the cold season based on the climatological distribution of sea-surface temperature (SST) and salinity gradients, as reported by Acha et al. (2020). To estimate the degree of overlap, we used the complete migratory-trip dataset. First, we created a spatial occurrence-density map from the trips of each penguin colony. Map cells had a resolution of 0.25° × 0.25°. We then converted density values to a scale ranging from 0 to 1 and retained cells with the highest occurrence values (1–0.3), removing low-occurrence cells. Finally, we overlaid these cells with the cells corresponding to each marine front, retaining the number of cells overlapping the front. This value was then divided by the total number of high-occurrence penguin cells to obtain a percentage overlap.

## RESULTS

### Migratory Trips of Magellanic Penguins (MPs) and Western Rockhopper Penguins (WRPs)

Maximum distance reached was best explained by the null model. However, both species and sex were included in the three additional models that were also considered plausible, but these variables were deemed non-informative because their 95% confidence intervals (CI) included zero (Supplementary Material Table 2; mean ± SD: WRP = 1208 ± 206 km, $n$ = 42; MP = 1166 ± 490 km, $n$ = 65).

Total distance traveled was greater in WRPs than in MPs (mean ± SD: WRP = 8651 ± 2360 km, $n$ = 39; MP = 6778 ± 2325 km, $n$ = 64; Fig. 1; Supplementary Material Table 2): according to the multimodel analysis, species was the only informative predictor (95% CI excluded zero; Supplementary Material Table 3), being the main factor in the best-supported models. Sex and the interaction between species and sex were present in the important models; however, they were considered non-informative. Post hoc analyses confirmed that differences between species were consistent for both sexes (WRP–MP contrast: Females: Estimate ± SE = 1901 ± 511, t-ratio = 3.72, $p < 0.00$; Males: Estimate ± SE = 1834 ± 511, t-ratio = 3.59, $p < 0.00$).

Angular direction was explained by a set of four models with AIC < 4 (Supplementary Material Table 2). One model included study year, species, and the interaction between both factors as predictors. Another model also included sex, and a final model additionally included the interaction between sex and species (Supplementary Material Table 2). However, only year and its interaction with species were informative predictors (95% CI excluded zero). The direction of all MP trips was, on average ± SD, 36.7 ± 24.5° NE (range = 32°–44.3°, $n$ = 65), whereas that of WRPs was 47 ± 32.6° NE (range = 36.3°–73.7°, $n$ = 42). Notably, in 2021, WRPs traveled at an angle of 73.7 ± 17.2° NE, moving farther east than usual (Fig. 2). This difference was statistically significant between WRPs in 2021 and MPs in 2022 and 2024 (Post hoc contrasts: WRP:2021–MP:2022 Estimate ± SE = 40.46 ± 10.76, t-ratio = 3.76, $p = 0.01$; WRP:2021–MP:2024 Estimate ± SE = 39.08 ± 11.36, t-ratio = 3.44, $p = 0.02$; Supplementary Material Table 3). The remaining contrasts were not significant ($0.11 < p < 1$; WRP:2021–WRP:2022 $p = 0.07$). In addition, neither sex nor its interactions contributed significant information to the model (Supplementary Material Table 3).

The model with the lowest AIC explaining migration departure date included sex, study year, species, and the interaction between species and year. However, four additional models were also important and included the interaction between species and sex (Fig. 1; Supplementary Material Table 2). Informative predictors were the year × species interaction, as well as year and species (all excluded zero in their 95% CI). MPs left the colony earlier than WRPs in all years (mean ± SD: WRP = 110 ± 8.17 days (~ April 20), $n$ = 45; MP = 99 ± 4.91 days (~ April 9), $n$ = 67), regardless of sex, with no significant differences between males and females within each species (sex contrasts: WRP $p$ = 0.61, MP $p$ = 0.57; Supplementary Material Table 3). Departure date showed a significant interaction between year and species ($p$ = 0.01; Supplementary Material Table 2). This effect was due to an exceptional delay in WRPs during 2021, when individuals departed for their wintering areas on average on day 116 ± 2 (~ April 26), significantly later than in 2019 (mean ± SE: 106 ± 2; Post hoc $p$ = 0.01) and 2024 (106 ± 2; Post hoc $p$ = 0.02). In contrast, MPs showed remarkable interannual stability in departure dates (mean range: 98–100; all interannual contrasts $p$ > 0.90). Because of this asymmetric shift, the temporal difference between both colonies doubled in 2021, reaching 16.1 days ($p$ < 0.00) compared to the 7.90 days observed in 2019 ($p$ = 0.02).

Arrival date at the colony (end of migration) was explained by two relevant models (AIC < 4) that included species, sex, study year, and the interaction between sex and species (Fig. 1; Supplementary Material Table 2). Species, year, and sex were informative predictors (95% CI excluded zero; Supplementary

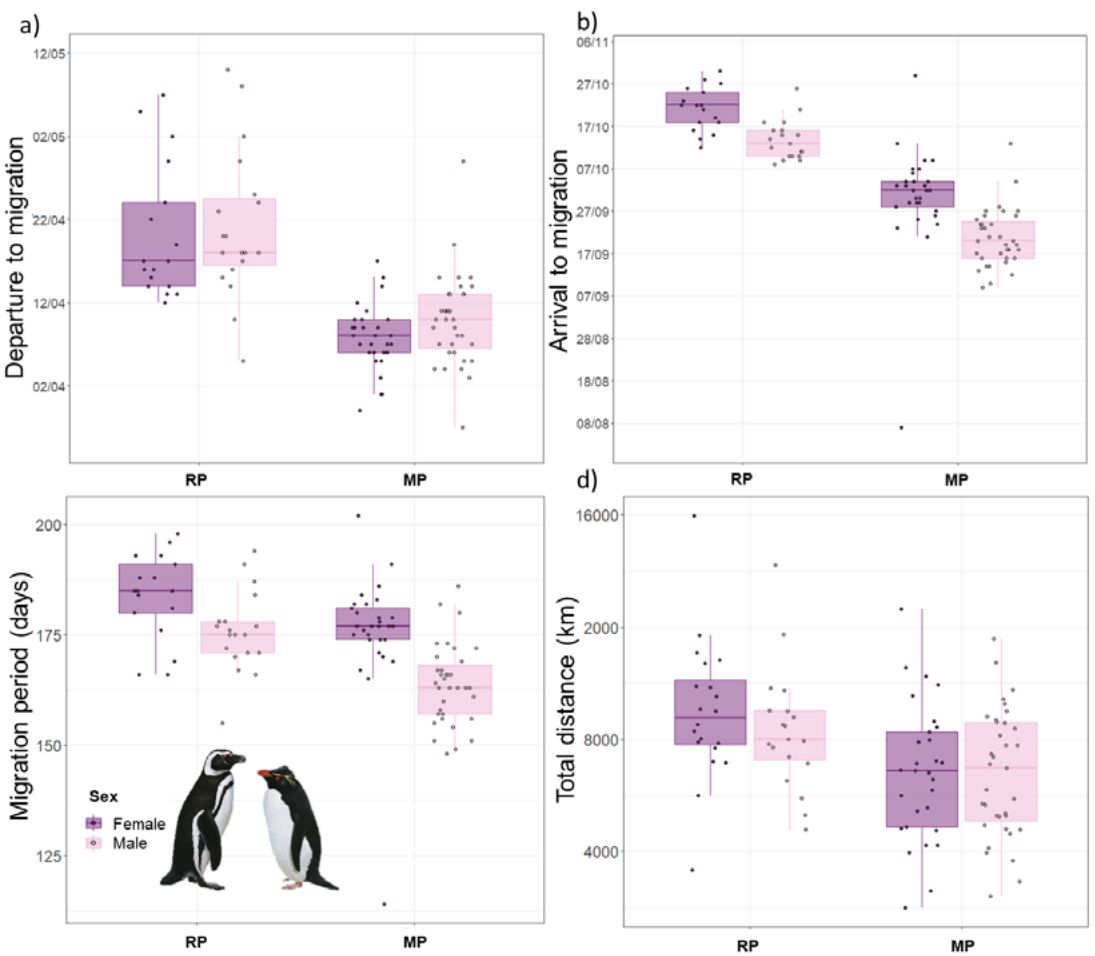


**Figure 1.** Characteristics of the migratory trips of Magellanic Penguins (*Spheniscus magellanicus*) from Isla Quiroga and Western Rockhopper Penguins (*Eudyptes chrysocome*) from Isla Pingüino, both breeding near Puerto Deseado, Argentina. Boxplots show sex differences in: (a) departure dates, (b) arrival dates (years pooled), (c) migration duration (total number of days), and (d) total distance traveled (km). Boxes represent the first and third quartiles (25% and 75%), lines within boxes indicate the median, whiskers indicate the interquartile range, and points represent individual values. Darker symbols correspond to females and lighter symbols to males.

Material Table 3). MPs arrived at colonies earlier than WRPs (Post hoc Estimate ± SE = 22 ± 1.70, t-ratio = 12.96, $p > 0.00$; mean ± SE: WRP = 290 ± 5.94 days (~ October 17), $n = 36$; MP = 268 ± 11 days (~ September 25), $n = 64$). Regarding annual variation, post hoc contrasts confirmed a significant difference between 2019 and 2022 among penguins (Estimate ± SE = 7.07 ± 2.09 days, t-ratio = 3.38, $p = 0.06$). The remaining interannual contrasts were not significant after adjustment for multiple comparisons ($p > 0.16$). Males always arrived earlier than females, regardless of species and year (Post hoc, Estimate ± SE = 8.25 ± 1.66, t-ratio = 4.96, $p < 0.00$). Thus, MP males were the first to arrive, followed by MP females, which arrived before WRP males, while WRP females were the last to complete migration (mean ± SE: Julian day: MP♂ = 264 ± 7, MP♀ = 274 ± 13, WRP♂ = 287 ± 4, WRP♀ = 294 ± 5; Supplementary Material Table 3).

The duration of the migratory period was explained by two models that included year, species, sex, and the sex × species interaction (Fig. 1; Supplementary Material Table 2). Among these predictors, the interaction was the only non-informative variable (95% CI included zero). Male migration lasted fewer days than female migration (mean ± SD: ♂ = 168 ± 11 days, $n = 54$; ♀ = 179 ± 13 days, $n = 46$; Supplementary Material Table 2). WRPs spent more days at sea than MPs (mean ± SD: WRP = 180 ± 10 days, $n = 36$; MP = 169 ± 13 days, $n = 64$). In addition, post hoc contrasts showed that migration lasted longer in 2019 than in 2021 and 2022 (respectively; $p = 0.04$, $p = 0.02$; Supplementary Material Table 3).

### Relationship Between Migratory Trips and Marine Fronts

These species used different areas of the continental shelf (Figs. 2 & 3). In addition, MPs used different areas depending on the breeding colony, with a tendency for individuals from more northern colonies to use more northern regions. WRPs used the El Rincón region, although during 2021 they also occupied the shelf-break area (Fig. 2).

The most heavily used front by penguins was the El Rincón Front, which was extensively visited by the northern and central MP colonies, as well as by a smaller proportion of individuals from southern colonies and by WRPs (Fig. 3, Table 1). The shelf-break

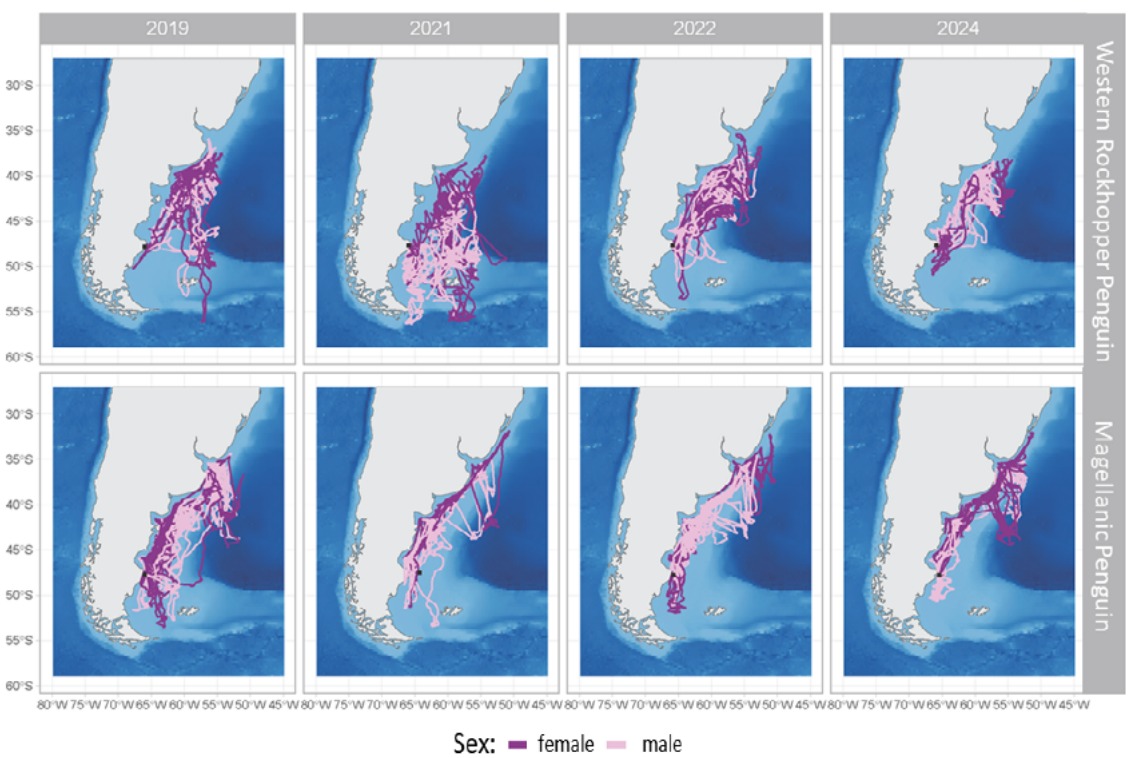


**Figura 2.** Migratory trips of Magellanic Penguins (*Spheniscus magellanicus*) from the Isla Quiroga colony and Western Rockhopper Penguins (*Eudyptes chrysocome*) from the Isla Pingüino colony, Santa Cruz, Argentina. Trips from the four years (2019, 2021, 2022, and 2024) for which data from both species were available are included. Colonies are indicated by black squares. Lighter tracks correspond to males and darker tracks to females. The x-axis shows longitude, and the y-axis shows latitude. Shades of blue indicate estimated sea depth.

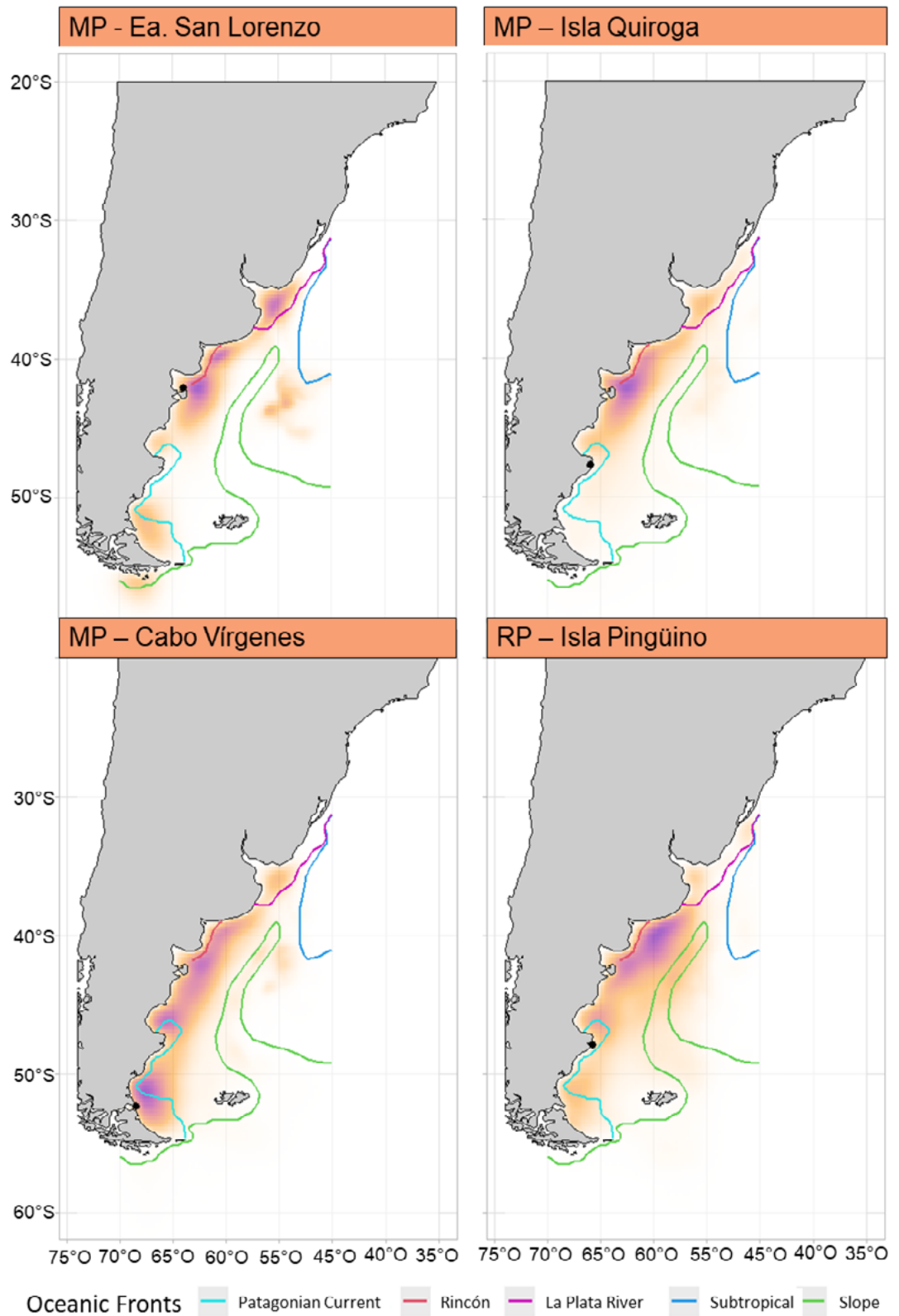


**Figura 3.** Occurrence density maps during migration for Magellanic Penguins (*Spheniscus magellanicus*; MP) from three colonies and Western Rockhopper Penguins (*Eudyptes chrysocome*; RP) breeding on Isla Pingüino. Occurrence was standardized from 0–1, where 1 represents the highest occurrence and 0 the lowest, and is displayed using a continuous color gradient from violet (1) to white (0). Colony locations are indicated by solid black circles. Colored lines represent different marine fronts, identified in the legend (modified from Acha et al. 2020).

front was used primarily by WRPs. The Patagonian Current Front was used to a lesser extent by central MPs and extensively by MPs from the southern portion of the distribution (Fig. 3, Table 1). The Río de la Plata Front did not overlap with the distribution of penguins from any of the colonies studied.

In this study, we found interspecific differences in the migratory trip characteristics of Magellanic Penguins (MP) and Western Rockhopper Penguins (WRP) breeding in very close colonies in Puerto Deseado. We also found differences in the intensity of marine front use according to colony and species. Particularly important for these species was the El Rincón Front region, which includes waters at the mouth of San Matías Gulf in Río Negro and those of southern Buenos Aires Province, and which also constitutes a Marine National Park and Nature Reserve.

Previous studies conducted at Isla Quiroga and Isla Pingüino have shown that MPs and WRPs partially share the areas used during migration, with greater overlap in their oceanographic niche (chlorophyll concentrations, temperature, salinity), but not in their isotopic niche—demonstrating differences in diet (Barrionuevo et al. 2025). To complete the understanding of migratory segregation, it was necessary to compare trip parameters. Regarding migratory trip characteristics, WRPs traveled nearly 2000 km more than MPs. This difference in distance is probably not due to a greater swimming capacity of WRPs, as they are even slightly smaller than MPs (Boersma et al. 2013, Pütz et al. 2013). In addition, WRPs dive to shallower average depths than MPs during the breeding season (Pütz et al. 2006b, Sala et al. 2014, Dehnhard et al. 2016, Rosciano et al. 2022). The difference cannot be explained by the maximum distance reached either, as we found no differences between species, nor by migration duration, because although WRP migration lasted 10 days longer than MP migration, this is insufficient to explain an additional 2000 km traveled. Therefore, the greater distance traveled is likely associated with greater daily movement by WRPs relative to MPs. In both species, females migrated longer than males, although this difference was much greater in MPs (15 more days versus 8 more days in WRPs). The difference in migration duration between sexes is explained by differences in arrival dates (MP males arrived 10 days earlier than females, and WRP males 7 days earlier than females), since departure dates were similar between sexes within species. In general, male penguins arrive earlier than females at nesting sites to prepare and defend their nests (Boersma et al. 2013). There were also differences between species in departure and arrival dates; MPs departed on migration approximately 11 days earlier than WRPs and also returned to the colony earlier than WRPs; the difference was 23 days between MP and WRP males and 17 days between females. This translates directly into a difference in the reproductive phenology of the species. At the study site, the average laying dates of first eggs are October 10 for MPs and November 7 for WRPs (Lera et al. 2023).

During migration, penguins would be expected to use marine fronts; however, given their diet, we would not expect complete overlap between marine fronts and penguin habitat use. MPs feed primarily on fish, such as *Engraulis anchoita* and *Sprattus fuegensis*, but also consume squid and crustaceans (Boersma et al. 2013, Ciancio et al. 2021). In contrast, WRPs feed at lower trophic levels, consuming larvae of those fish species, squid, and crustaceans (Pütz et al. 2013). In this regard, we found that different colonies used the fronts of the Argentine shelf differently. WRPs from Isla Pingüino used fronts to a lesser extent than MPs. Only 15% of the most heavily used WRP locations overlapped with the El Rincón Front and 8% with the shelf-break front. However, the El Rincón region was the area most used by this species. The shelf-break front region was particularly important in 2021, when positive sea surface temperature anomalies occurred (Barrionuevo et al. 2025), demonstrating its potential importance as a refuge under global warming scenarios.

**Table 1.** Use of marine fronts on the Argentine continental shelf by Western Rockhopper Penguins (*Eudyptes chrysocome*) and Magellanic Penguins (*Spheniscus magellanicus*) (shown by colony). Values are expressed as the percentage that each front represents within the total number of highest-use cells for each colony.

| Especie | Front Colony | Patagonian Current | El Rincón | Slope | Subtropical | La Plata River |
|---|---|---|---|---|---|---|
| Western Rockhopper Penguins | Isla Pingüino | 0.00 | 15.38 | 7.59 | 0.00 | 0.00 |
| Magellanic Penguins | San Lorenzo | 0.00 | 92.31 | 0.00 | 0.00 | 0.00 |
| | Isla Quiroga | 1.61 | 69.23 | 0.00 | 0.00 | 0.00 |
| | Cabo Vírgenes | 40.32 | 15.38 | 0.00 | 0.00 | 0.00 |

For MPs, we could divide the Argentine breeding population into three groups (excluding the Malvinas Islands population) according to available information on colony location, population size, and migration patterns. 1) Northern colonies, represented in this study by Estancia San Lorenzo, would include those in Río Negro and Chubut (García-Borboroglu et al. 2022) and account for 62.4% of the total Argentine population. In this case, MP distribution overlapped extensively with the El Rincón Front. Although it did not overlap with another front, the Río de la Plata Front, which constitutes the eastern boundary of the river plume (Piola et al. 2008), appears to act as an eastern boundary for these individuals as well. This front separates estuarine waters from marine waters; penguins using the region west of this front are probably capturing prey of estuarine or coastal origin. 2) Colonies in the central portion of the MP breeding distribution could include those from northern and central Santa Cruz, from Punta Pájaros to Monte León (Millones et al. 2021), and comprise 21.4% of the total population. Penguins from the center of the distribution are represented in this study by the Isla Quiroga colony and primarily used the El Rincón Front (70%) and, to a lesser extent, the Patagonian Current Front (1.6%). 3) Finally, southern colonies, including those from southern Santa Cruz (Millones et al. 2021) and Tierra del Fuego (Raya Rey et al. 2004), represent 16.2% of the population. This group is represented in our study by the Cabo Vírgenes colony, whose penguins used the Patagonian Current Front (40%) and the El Rincón Front (15%).

The northern (1) and central (2) sectors of the MP breeding distribution, which comprise most of the population, as well as the WRP colony studied, preferentially used the El Rincón area. This front extends approximately from 39°S to 41°S, is located in shallow coastal waters, and is present year-round (Acha et al. 2004). It is situated off the south-southeastern coast of Buenos Aires Province and includes the mouth of San Matías Gulf. This area represents one of the country's most important hydrocarbon development zones, including the Bahía Blanca petrochemical complex, and soon it will be developed as an oil and gas loading area, with the installation of offshore buoys and degassing vessels in San Matías Gulf. On the other hand, it is an area of relatively low fishing effort, with seasonal fishing closures during much of the year (Copello et al. 2014). Both the industrial bottom-trawl fleet and the artisanal longline fleet operate here. The former operates year-round, although with lower effort during the winter months when penguins use these waters. Nevertheless, direct or indirect interactions may occur in the area through incidental penguin bycatch or even through the capture of non-target species such as the Argentine Anchovy (see Gandini et al. 1998). Although there are records of incidental penguin bycatch in Argentine Hake (*Merluccius hubbsi*) and Patagonian Red Shrimp (*Pleoticus muelleri*) trawl fisheries, its incidence does not appear to be very high (Gandini et al. 1998, González-Zeballos & Yorio 2006, Crawford et al. 2017).

The northern colonies of the MP distribution, which represent 62% of the population analyzed in this study, used the Río de la Plata estuary region. The Río de la Plata plume forms a low-salinity, nutrient-rich area whose extent depends primarily on river discharge and wind intensity and direction (Piola et al. 2008). It has been reported that variation in plume extent strongly influenced the reproductive success of MPs at Punta Tombo (Rebstock & Boersma 2018), a colony belonging to the northern sector according to our categorization of the species' national distribution. In terms of commercial fishing, this area is important for both offshore and coastal fresh-fish fleets. It is a fishing ground for some penguin prey species, although overall fishing effort and total catches are not high (Copello et al. 2014). There are few records of direct interactions between penguins and these fleets (e.g., Tamini et al. 2002, Seco Pon et al. 2013).

The shelf-break front, which was used primarily by WRPs during anomalous years, is a permanent front extending along the continental shelf break from Burdwood Bank eastward, around the Malvinas Islands, and northward to the confluence of the Malvinas and Brazil Currents (Acha et al. 2004). There are two major fisheries in this region, targeting Argentine Hake and Argentine Shortfin Squid (*Illex argentinus*), but available data indicate that neither has a significant direct effect on penguins in the area (Tamini et al. 2015, Crawford et al. 2017). In contrast, the Patagonian Current Front was heavily used by the southern sector of the MP distribution, although this sector represents only 16% of the population studied. This front is critical for the breeding and distribution of adult penguin prey species such as the Fuegian Sprat (*Sprattus fuegensis*; Madirolas et al. 2000) and *Grimothea gregaria* (Diez et al. 2016).

In summary, fronts associated with the waters of Buenos Aires Province appear to be key feeding areas for penguins, particularly MPs, during the non-breeding period. WRPs also use these fronts, although to a much lesser extent. Fortunately, commercial fisheries do not currently appear to represent a major problem

during the winter months for penguins using this region, either through competition for prey or bycatch (Crawford et al. 2017). Identifying the areas most heavily used during penguin migration and ensuring their protection, particularly from large-scale extractive activities, is essential for the conservation of penguins breeding in the Argentine Sea. This is especially important in the context of expanding hydrocarbon development on the continental shelf and ongoing global change, for which there is already evidence of impacts on marine areas of the Argentine continental shelf (Franco et al. 2020).

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## SUPPLEMENTARY MATERIAL

You can access the supplementary material for this article by visiting the link: https://doi.org/10.56178/eh.v41i1.1537.

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# BIRDS IN THE CONCRETE FOREST: NEST-SITE USE ON HUMAN-MADE STRUCTURES ACROSS WESTERN ECUADOR

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**ABSTRACT:** Urban expansion is a major driver of habitat transformation, reducing the availability of natural nesting sites for birds and promoting the use of anthropogenic structures. In this study, we document nesting behavior of native bird species in human-made structures across Western Ecuador, a region experiencing rapid urban growth and significant ecosystem fragmentation. We combined field observations (2023–2025), detailed monitoring of two focal species (*Tyrannus niveigularis* and *Myrmia micrura*) in 2025, and participatory science data from the iNaturalist platform (2009–2025). We compiled 49 nesting records from 15 species using a wide variety of artificial substrates including walls, light poles, roofs, cables, and air conditioning units. Detailed observations revealed successful reproduction in both focal species including nest reuse and biparental care by *T. niveigularis* and repeated nesting attempts by *M. micrura* on an unconventional artificial substrate. Our findings include novel records of anthropogenic nesting for three species and expand existing knowledge of urban nesting ecology in the region. While artificial structures may provide alternative nesting opportunities, they can also expose birds to risks such as disturbance, predation, and reduced reproductive success. These results highlight the importance of urban environments as emerging ecological systems and underscore the value of integrating field observations with participatory science data to better understand species responses to human-modified landscapes in tropical regions.

**KEYWORDS:** *bird nesting, participatory science, urban birds, urbanization*

Urban expansion is one of the most pervasive drivers of environmental change, reshaping landscapes and altering ecological processes worldwide (Chace & Walsh 2006, McKinney 2008, Reynolds et al. 2019). For birds, these transformations often result in the loss of natural nesting substrates and the increase of predator-exposure, forcing individuals to adjust their reproductive strategies in increasingly human-dominated environments (Marzluff 2001, Farwell & Marzluff 2013). One of the most conspicuous responses is the use of anthropogenic structures for nesting. Several bird species nest on artificial substrates such as lamp posts, building facades, electric poles, and other anthropogenic structures (Turner & Rose 1989, Wang et al. 2015, Baptista et al. 2020, 2024a, 2024b, León-E et al. 2024).

While such behavior may allow birds to survive in altered landscapes, human-made structures can act as ecological traps offering seemingly suitable conditions that ultimately reduce fitness due to exposure to pollutants, nest disturbance, electrocution, collisions, and higher risk of depredation by domestic animals (Mainwaring 2015, Bauerová et al. 2017, Van Doren et al. 2021). Although some urban areas might provide shelter (Martin 1993), the reproductive success in cities tends to be lower than in natural or rural habitats (Rodewald et al. 2013).

Despite growing interest in urban bird ecology globally, information on nesting behavior on anthropogenic structures remains limited across Western Ecuador (a.k.a. The Coast locally). This biodiverse region, between the Andes and the Pacific Ocean, has experienced extensive habitat loss and fragmentation with rapid and often unplanned urban expansion

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reshaping native ecosystems (Cuesta et al. 2017, Rivas et al. 2021). In this study, we aim to document and describe nesting events of native birds using human-made structures across Western Ecuador. Specifically, we: (1) monitored in detail the nesting of two focal species (*Tyrannus niveigularis* and *Myrmia micrura*) through constant field observations; (2) compiled opportunistic field records of additional species nesting on anthropogenic substrates to characterize the diversity of nesting strategies observed in situ; and (3) integrated participatory science data from the iNaturalist platform to identify additional cases.

## METHODS

### Study Area

This study was conducted in the region of Western Ecuador. This area extends from the foothills of the western Andes to the Pacific Ocean, approximately between 1°20'N and 3°45'S latitude (Fig. 1), and encompasses a wide range of ecosystems. In the north, Western Ecuador is limited by the Chocó rainforest, and in the south, by the coastal desert of Peru. The north is characterized by high annual rainfall and dense evergreen vegetation. Toward the central and southern portions, the landscape transitions into equatorial seasonally dry forests and semi-arid xeric shrublands which are defined by lower precipitation and predominantly deciduous vegetation (Dodson & Gentry 1991, MAE 2013). The warm and rainy season occurs between December and May and the cold and dry season between June and November. This seasonality shapes species composition, distribution and reproductive behavior (Marchant 1960, Armijos-Ojeda et al. 2021).

The Coast is the region with the largest conservation gaps and irreversible land use changes in Ecuador (Lessmann et al. 2014). Tropical forests in this region have experienced severe habitat loss with over 90% of the original forest cover now deforested or fragmented (Dodson & Gentry 1991). This process has led to the widespread transformation of native coastal ecosystems, such as mangroves, wetlands, and dry forests, into urban areas, shrimp farms, and agricultural fields (Carvajal & Alava 2007, Hamilton & Stankwitz 2012, Cuesta et al. 2017, Rivas et al. 2021). The Coast is poorly represented within Ecuador's national system of protected areas (Lessmann et al. 2014), further exacerbating their fragility and the risk of biodiversity loss (Sierra et al. 2002, Portillo-Quintero & Sánchez-Azofeifa 2010, Manchego et al. 2017, Rivas et al. 2024).

As in many parts of Latin America, urban expansion in Ecuador has occurred rapidly and often without long-term land use planning (Lippe et al. 2022, Noh et al. 2022). These changes are particularly pronounced around major cities (Dalmasso & Fillón 1972, Curillo & Hidalgo 2011, Baker 2012, Delgado 2013, Parés-Ramos et al. 2013, Bonilla Mena et al. 2021, Coronel & Nicole 2022, Mena et al. 2022, Lager 2023). The remaining forest fragments are highly vulnerable to human pressures such as agricultural expansion, cattle ranching, logging, mining, and continued urbanization (Sáenz & Onofa 2005).

### Study Species

We focused on the most common native bird species with the highest number of nesting records in the urban areas of Western Ecuador. We excluded wading and marine birds and non-native bird species such as the House Sparrow (*Passer domesticus*) and the Common Pigeon (*Columba livia*). To identify the most common bird species in urban environments, we selected bird records from iNaturalist based on whether they were located within or outside the shapefiles of urban and periurban areas (Instituto Geografico Militar 2022). For subsequent searches of bird nesting events, we focused on the most common species identified in this analysis.

### Data Collection

We compiled constant field observations of two species which were monitored in detail whenever possible through ecological and behavioral notes, and casual observations by the authors when they detected the presence of a bird nesting event on human-made structures. The constant field observations were in 2025 with casual observations between 2023 and 2025. For the participatory science records, we compiled observations from the iNaturalist platform between 2009 and 2025, selecting observations from bird species based on two requirements: 1) nesting evidence of birds in any type of human structure such as walls, light poles, air conditioners, tubular, metal, or wooden posts, and furniture amongst others; and 2) location within the iNaturalist region called 'Ecuadorian Pacific Lowlands'. This project's area consisted of the ecosystems of Ecuador that are located west of the Andes and below 1500 m.a.s.l., using the shapefiles of the Ministry of Environment and Energy of Ecuador (MAE 2013). Those records that met the selection criteria were manually added to the project 'Aves en Estructuras Humanas Ecuador' (inaturalist.org/projects/aves-en-estructuras-humanas-ecuador).

## RESULTS

After revision, we compiled a total of 49 nesting records from 15 species using both direct observation and iNaturalist records: *Columbina buckleyi*, *Columbina cruziana*, *Zenaida auriculata*, *Amazilis amazilia*, *Doryfera ludovicae*, *M. micrura*, *Forpus coelestis*, *Petrochelidon rufocollaris,* *Progne chalybea*, *Pygochelidon cyanoleuca*, *Furnarius cinnamomeus*, *T. niveigularis*, *Troglodytes musculus*, *Mimus longicaudatus*, and *Sicalis flaveola* (Fig. 1, Table 1). We documented nesting sites of nine different bird species directly during fieldwork. From these, we monitored in detail two bird species (*T. niveigularis*, and *M. micrura*), described as case studies, and photographed 12 casual records for seven bird species (*Z. auriculata*, *F. coelestis*, *F. cinnamomeus*, *P. chalybea*, *T. musculus*, *M. longicaudatus*, and *S. flaveola*) nesting on anthropogenic structures across coastal Ecuador. Additionally on the iNaturalist platform, 34 observations from 10 of the 15 selected species showed anthropogenic nesting behavior. We did not find records of nesting events of raptors (Accipitriformes and Falconiformes) or woodpeckers (Picidae). Two observers generated the constant field observations, all the authors (4) recorded the casual ones and 22 iNaturalist users generated the records presented in this study.

### Nest monitoring cases

Snowy-throated Kingbird (*Tyrannus niveigularis*):

We documented nesting and reuse of a nest by Snowy-throated Kingbirds across two consecutive breeding seasons (2024–25) in a periurban residential area of Manta, Manabí Province (0°57'S, 80°45'W). The nest was located at the intersection of electrical cables and a metallic bracket attached to a concrete streetlight post. The nest consisted of dry twigs, grass stems, and fine roots loosely interwoven and wedged into a small recess formed between horizontal and vertical cables (Fig. 2).

In 2024, we observed two adults constructing the nest and one of them incubating between February 9 and 14 (Fig. 2A). However, no nest monitoring was carried out that year. In the 2025 season, nest maintenance and material delivery started on February 8 (Fig. 2B) and one adult was documented incubating by February 19. The pair periodically returned to the nest carrying twigs. Later on March 7, we observed an

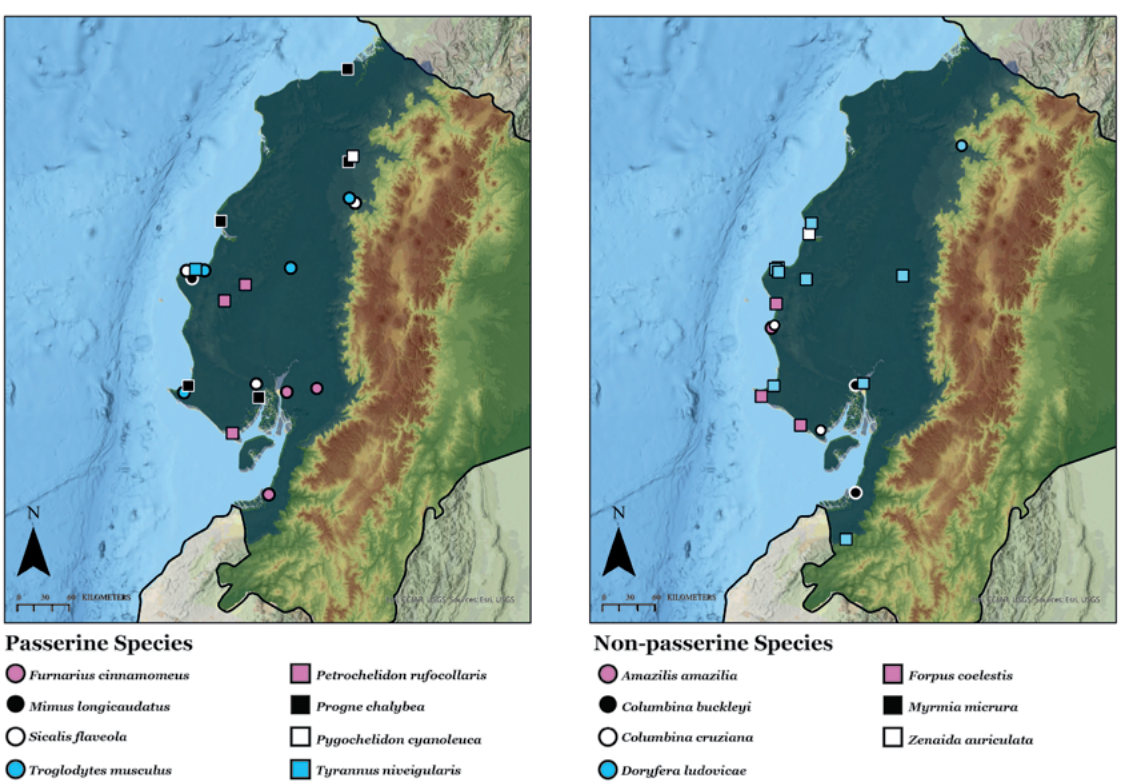


**Figure 1.** Distribution of records of bird nesting records across the Western Ecuador region. The blue silhouette shows the extension of the study region. Maps show observations of passerine (left) and non-passerine birds (right).

adult removing a fecal sac from the nest while faint chick calls were audible, suggesting successful hatching. On March 12, three nestlings were photographed (Fig. 2C) confirming the presence of a brood. Care was biparental: both adults alternated foraging trips and nest guarding. When Tropical Kingbirds (*Tyrannus melancholicus*) or other passerines approached the area, the Snowy-throated Kingbirds displayed aggressive territorial behavior. On March 16, we observed them defending the nest from an icterid (Fig. 2D), most likely *Dives warszewiczi*, and feeding the chicks a dragonfly (Fig. 2E). We also saw the chicks being fed butterflies (e.g., *Dione vanillae*), katydids (Tettigoniidae) and small insects (Fig. 2F). We observed occasional fecal sac removal with adults collecting them directly from the cloaca as chicks flexed and expelled waste, demonstrating typical nest sanitation behavior. Nestlings were vocal, frequently begging with open mouths and raised heads.

By March 21, the chicks had grown noticeably, displaying adult-like plumage including a dark facial mask, pale underparts, and brownish wings with yellowish bellies (Fig. 2G). On March 26, we recorded all three fledglings perched in a large *Samanea saman* tree with its base approximately 15 m from the nest but with branches extending closer to it (Fig. 2H), suggesting that fledging had occurred recently. Although they did not return to the nest, the fledglings continued to receive parental care through later dates. We observed the three fledglings until the last days of March when observations ended. Overall, the incubation period was approximately 17 days while the nesting period lasted for about 19 days. In 2026, no nest of this species was recorded on that light pole. We found no records of Snowy-throated Kingbirds nesting on human-made structures on the iNaturalist platform.

Short-tailed Woodstar (*Myrmia micrura*):

We recorded two consecutive nest observations of Short-tailed Woodstars in Bahía de Caráquez, Manabí (0°35'S, 80°25'W), both in the same structure: a horizontal green plastic tube (Fig. 3A), part of a hanging decorative ornament (a rattle) surrounded by potted plants and adjacent to a patio of a white house. We first observed the nest construction in early March 2025 which took approximately around a week to complete. The female incubated the eggs for about 16 days and two chicks successfully hatched. The juveniles left the nest approximately two weeks after hatching. Around three weeks later, the female returned to the same nest, performed repairs, and initiated a second breeding attempt. This second clutch, recorded on April 28, also consisted of two eggs. However, the nest was subsequently abandoned, most likely due to disturbance caused by gardening work involving machinery.

**Table 1.** List of nesting events in Western Ecuador from participatory science observations.

| Species | Location | Year | Nesting structure | Reproductive outcome | Source | Observer |
|---|---|---|---|---|---|---|
| *Columbina buckleyi* | Guayaquil, Guayas | 2020 | Wall | Not observed | iNaturalist | María Verónica Núñez Gallegos |
| *Columbina buckleyi* | Machala, El Oro | 2023 | Wall and cables | Two chicks in nest | iNaturalist | Roy Alexander Zambrano Morales |
| *Columbina cruziana* | Puerto López, Manabí | 2020 | Roof gutter | Not observed | iNaturalist | Frank Dietze |
| *Columbina cruziana* | El Morro, Guayas | 2023 | Metal beam | Two chicks fledged | iNaturalist | Benjamín Navas |
| *Zenaida auriculata* | Portoviejo, Manabí | 2019 | Metal beam (roof) | Not observed | iNaturalist | Jaime Camacho |
| *Zenaida auriculata* | Guayaquil, Guayas | 2019 | Wall and metal structure | Not observed | iNaturalist | Jaime Camacho |
| *Zenaida auriculata* | Guayaquil, Guayas | 2020 | Window wall opening | Not observed | iNaturalist | Jaime Camacho |
| *Zenaida auriculata* | Quevedo, Los Ríos | 2021 | Roof | Not observed | iNaturalist | Arianna Alava |

| Species | Location | Year | Nesting structure | Reproductive outcome | Source | Observer |
|---|---|---|---|---|---|---|
| *Zenaida auriculata* | El Bunque, El Oro | 2021 | Air conditioning unit | One chick observed | iNaturalist | lexypizarro |
| *Zenaida auriculata* | Canoa, Manabí | 2023 | Bamboo roof | Not observed | iNaturalist | David Torres |
| *Zenaida auriculata* | Punta Blanca, Santa Elena | 2024 | Wall | Not observed | iNaturalist | Jaime Camacho |
| *Amazilis amazila* | Puerto López, Manabí | 2009 | Cables / lighting wires | Not observed | iNaturalist | Jeremy Baker |
| *Doryfera ludovicae* | Palma Real, Pichincha | 2017 | Roof | Not observed | iNaturalist | Edison Ocaña |
| *Doryfera ludovicae* | Palma Real, Pichincha | 2018 | Roof | Not observed | iNaturalist | Edison Ocaña |
| *Forpus coelestis* | Salinas, Santa Elena | 2023 | Wooden post | Six eggs, outcome unknown | iNaturalist | Assad Guerra |
| *Petrochelidon rufocollaris* | General Villamil, Guayas | 2022 | Wall | Not observed | iNaturalist | Juan Romero |
| *Petrochelidon rufocollaris* | Honorato Vásquez, Manabí | 2022 | Wall | Not observed | iNaturalist | Pedro Manzaba |
| *Petrochelidon rufocollaris* | Sucre, Manabí | 2023 | Wall | Not observed | iNaturalist | Jaime Camacho |
| *Petrochelidon rufocollaris* | General Villamil, Guayas | 2023 | Wall | Not observed | iNaturalist | Humberto Bonilla |
| *Petrochelidon rufocollaris* | Sucre, Manabí | 2024 | Wall | Not observed | iNaturalist | Pier Luigi Maquilon |
| *Progne chalybea* | Las Peñas, Esmeraldas | 2017 | Streetlight post | One chick observed | iNaturalist | Edison Ocaña |
| *Progne chalybea* | Chongón, Guayas | 2022 | Metal beam | One juvenile observed | iNaturalist | Diana Cárdenas |
| *Progne chalybea* | Puerto Quito, Pichincha | 2023 | Wooden beam on wall | Not observed | iNaturalist | Don Wellmann |
| *Progne chalybea* | Punta Blanca, Santa Elena | 2024 | Wall | Two chicks observed | iNaturalist | Jaime Camacho |
| *Pygochelidon cyanoleuca* | Puerto Quito, Pichincha | 2021 | Roof | Three hatchlings observed | iNaturalist | Luis Valle |
| *Furnarius cinnamomeus* | Naranjito, Guayas | 2018 | Wooden post | Not observed | iNaturalist | Marco Durán |
| *Furnarius cinnamomeus* | Delia, Guayas | 2023 | Wooden post | Not observed | iNaturalist | Jorge Abad Lozano |
| *Troglodytes musculus* | Santo Domingo, SDT | 2019 | Furniture | Five eggs observed | iNaturalist | Fundación Madre Yumbo |
| *Troglodytes musculus* | Carlos Julio Arosemena, Los Ríos | 2015 | Wooden post | Not observed | iNaturalist | josefocj |

| Species | Location | Year | Nesting structure | Reproductive outcome | Source | Observer |
|---|---|---|---|---|---|---|
| *Troglodytes musculus* | Ballenita, Santa Elena | 2023 | Plastic tube | Not observed | iNaturalist | Assad Guerra |
| *Sicalis flaveola* | Santo Domingo, SDT | 2019 | Streetlight post | Not observed | iNaturalist | David Torres |
| *Sicalis flaveola* | Cerro Blanco, Guayas | 2018 | Wooden post (roof) | Not observed | iNaturalist | Benjamín Navas |
| *Zenaida auriculata* | Manta, Manabí | 2025 | Air conditioning unit | Not observed | Casual field observation | Daniel Velasco Cedeño |
| *Zenaida auriculata* | Manta, Manabí | 2025 | Streetlight post | Not observed | Casual field observation | Elías Viteri-Basso |
| *Zenaida auriculata* | Manta, Manabí | 2025 | Streetlight post | Not observed | Casual field observation | Daniel Velasco Cedeño |
| *Zenaida auriculata* | Manta, Manabí | 2025 | Streetlight post | Not observed | Casual field observation | Daniel Velasco Cedeño |
| *Forpus coelestis* | Cayo Paraíso, Manabí | 2023 | Roof | Not observed | Casual field observation | Elías Viteri-Basso |
| *Forpus coelestis* | General Villamil, Guayas | 2023 | Roof | Not observed | Casual field observation | Ariel Guerrero Campoverde |
| *Forpus coelestis* | Manta, Manabí | 2025 | Roof | Not observed | Casual field observation | Daniel Velasco Cedeño |
| *Forpus coelestis* | Manta, Manabí | 2025 | Streetlight post | Not observed | Casual field observation | Daniel Velasco Cedeño |
| *Progne chalybea* | Canoa, Manabí | 2023 | Wall | Not observed | Casual field observation | Walter Vivas |
| *Progne chalybea* | Manta, Manabí | 2025 | Roof (tile openings) | Not observed | Casual field observation | Daniel Velasco Cedeño |
| *Furnarius cinnamomeus* | Machala, El Oro | 2025 | Light post | Not observed | Casual field observation | Walter Vivas |
| *Troglodytes musculus* | Manta, Manabí | 2025 | Wall | Not observed | Casual field observation | Daniel Velasco Cedeño |
| *Mimus longicaudatus* | Manta, Manabí | 2025 | Air conditioning unit | Not observed | Casual field observation | Daniel Velasco Cedeño |
| *Sicalis flaveola* | Manta, Manabí | 2025 | Air conditioning unit | Not observed | Casual field observation | Daniel Velasco Cedeño |
| *Myrmia micrura* | Bahía de Caráquez, Manabí | 2025 | Hanging decorative swing | Two successful fledglings | Constant field monitored | Leonardo Viteri Velasco & Daniel Velasco Cedeño |
| *Tyrannus niveigularis* | Manta, Manabí | 2024 | Streetlight post | Not observed | Constant field monitored | Daniel Velasco Cedeño |
| *Tyrannus niveigularis* | Manta, Manabí | 2025 | Streetlight post | Three fledglings | Constant field monitored | Daniel Velasco Cedeño |

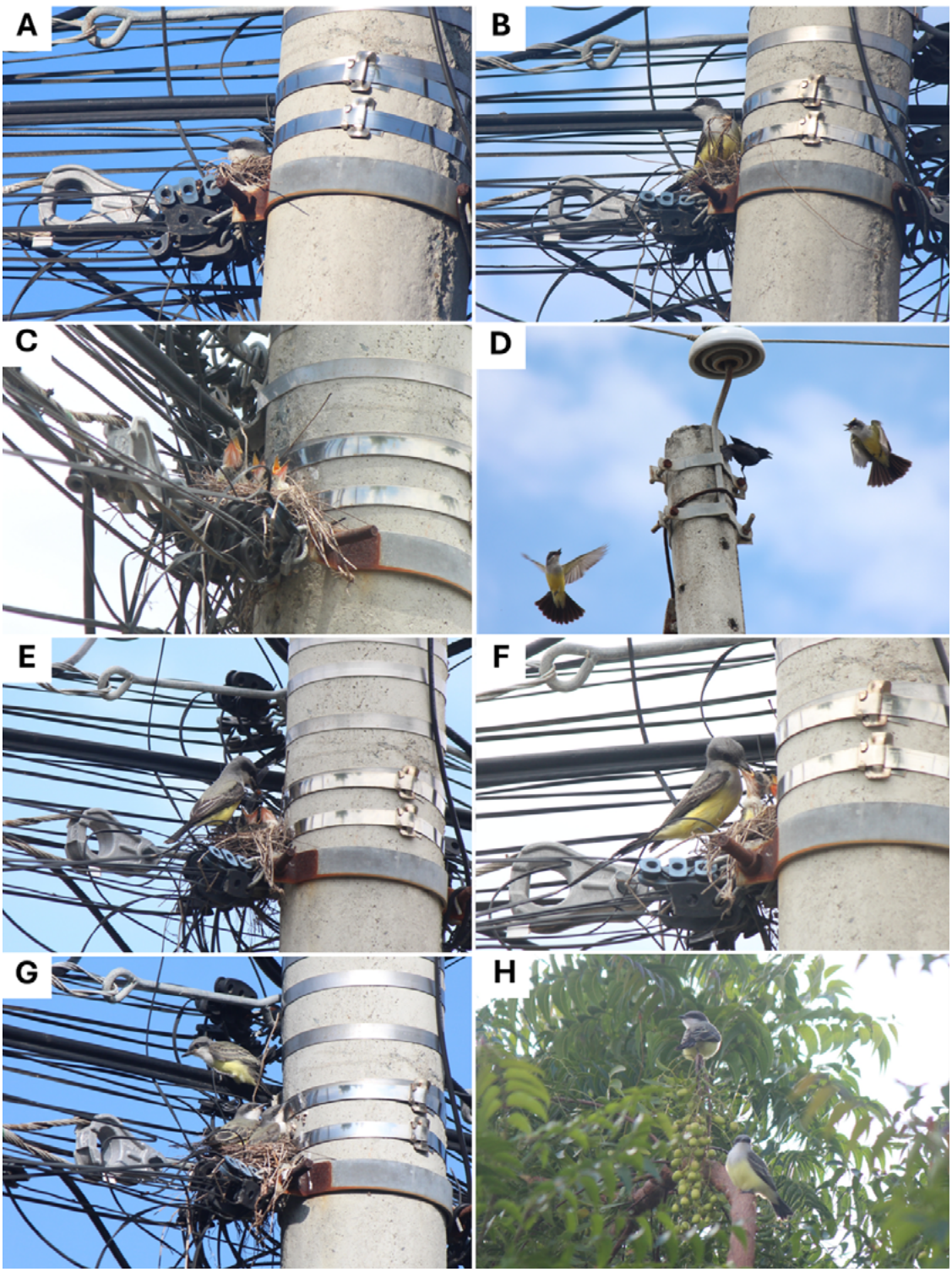


**Figure 2.** Photographic records of the nesting events of *Tyrannus niveigularis* in Manta, Manabí Province, Ecuador, at the same lamp post in A) 2024 and B–H) 2025. Photographs: Velasco-Cedeño D.

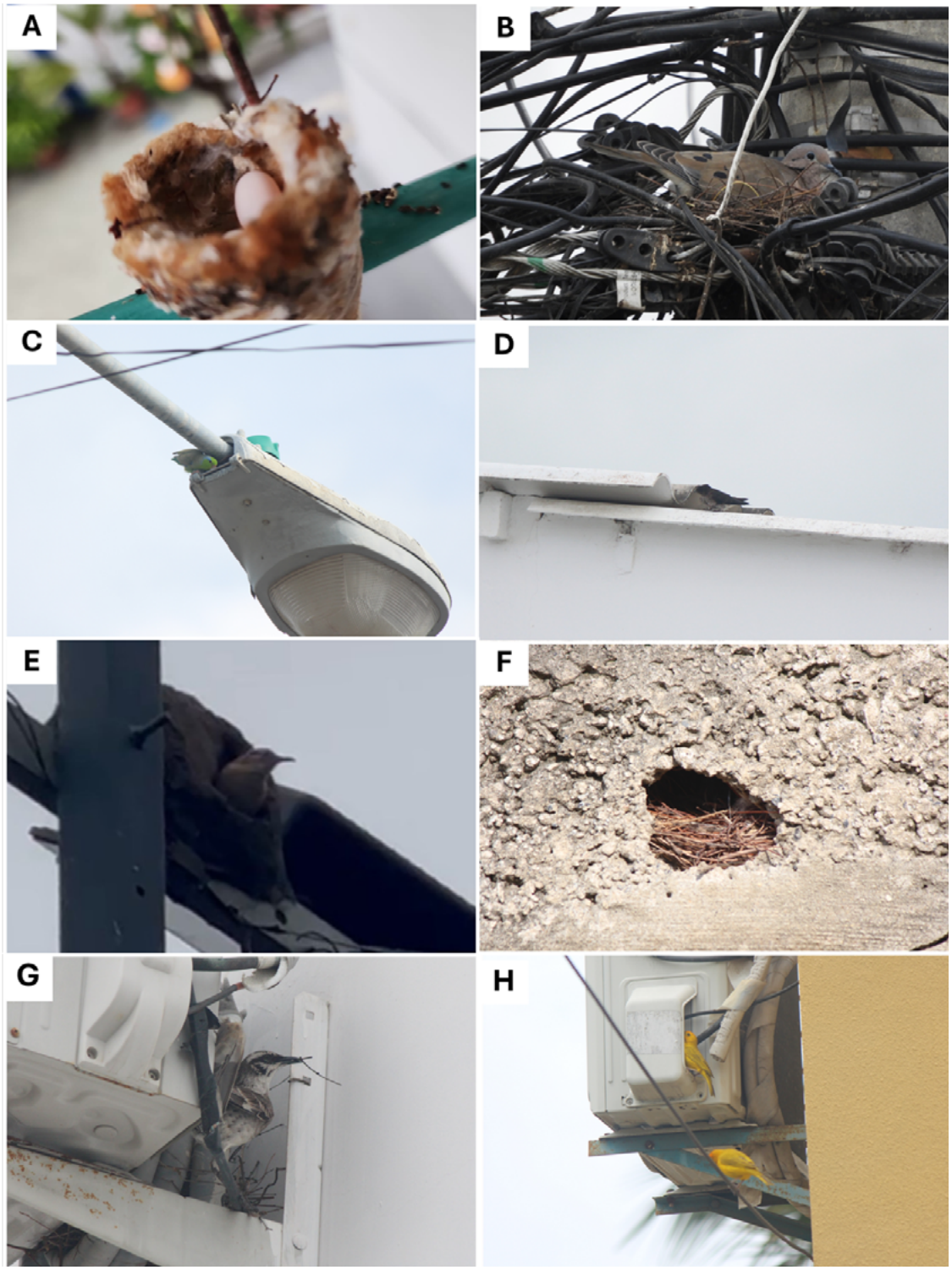


**Figure 3.** Photographic records of bird nesting events on human-made structures across Western Ecuador: A) *Myrmia micrura*, B) *Zenaida auriculata*, C) *Forpus coelestis*, D) *Progne chalybea*, E) *Furnarius cinnamomeus*, F) *Troglodytes musculus*, G) *Mimus longicaudatus* and H) *Sicalis flaveola*. Photographs: A) Viteri B) Viteri-Basso E., C–D and F–H) Velasco-Cedeño D, E) Vivas W.

### Nest field observations

Eared Dove (*Zenaida auriculata*):

We documented four nesting observations of Eared Dove, three of which involved adult individuals actively nesting or incubating in Manta, Manabí. The first record on January 27 2025 involved an individual nesting on a streetlight post among electrical cables (Fig. 3B) located on a busy street surrounded by tall apartment buildings and hotels (0°56'S, 80°44'W). The others were observed in a periurban residential neighborhood (0°57'S, 80°45'W). One individual was perched on its nest built on a tangle of electric cables on a concrete pole. The nest was a simple structure of thin branches. The other individual was nesting and incubating on an air conditioning vent attached to the back wall of a house. Additionally, we recorded an empty nest with a single egg placed at the edge, located on a larger lamp post on an avenue near a children's green area in the same periurban neighborhood as the previous observations.

Pacific Parrotlet (*Forpus coelestis*):

We recorded two nesting observations of Pacific Parrotlet on human-made wooden cabins along the coast. The first record was documented on December 29 2023 in Cayo Paraíso, Manabí (1°18'S, 80°45'W). The second record was on July 11 2023 in Puerto Engabao, a coastal community in the Canton of Playas, Guayas Province (2°33'S, 80°30'W). In both cases, a male and a female were observed actively moving back and forth from the nest.

In Manta, Manabí, two additional cases of Pacific Parrotlet using human structures were observed on February 19 2025. One individual was recorded at the entrance of a cavity in the roof of a house, while a pair was seen entering a lamp post (Fig. 3C). Both records were from the same location (0°57'S, 80°45'W) along the main avenue of a periurban residential area.

Gray-breasted Martin (*Progne chalybea*):

One adult Gray-breasted Martin was recorded nesting in a cavity on a house in an urban area (Fig. 3D). This observation was made on December 27 2023 in Canoa, Manabí (0°27′S, 80°27′W). A male and a female were observed perched on a plastic tube near the nest in a non-active state. In Manta, at least three individuals were observed entering the wavy cavities in between roof tiles of houses in a periurban residential area while scanning their surroundings (0°57'S, 80°45'W).

Pacific Hornero (*Furnarius cinnamomeus*):

We recorded a case of Pacific Hornero nesting on a light post at a basketball court (Fig. 3E) on January 12 2025 in San Patricio, Machala, El Oro Province (3°16'S, 79°55'W). The site was a private residential area characterized by open spaces with green areas, trees, and nearby shrubs. The nest was built around the metal structure at the intersection of two posts. A single individual was observed inside the nest, but due to the species' monomorphic characteristics, its sex could not be determined. The bird was later observed foraging on the observation wall before flying toward nearby trees.

Southern House Wren (*Troglodytes musculus*):

On March 7 2025, a nest of Southern House Wren was observed built inside a small circular cavity in a rough-textured concrete wall (Fig. 3F) in a periurban residential neighborhood of Manta, Manabí (0°57'S, 80°45'W). The cavity entrance measured only a few centimeters in diameter and contained a compact nest composed mainly of fine, dry twigs tightly arranged to fill the internal space, providing shelter within the wall structure. Adult wrens at this site displayed marked territorial behavior: when approached at approximately 10 meters, the birds became visibly agitated and began vocalizing persistently, producing loud and repetitive calls while moving between nearby perches.

Long-tailed Mockingbird (*Mimus longicaudatus*):

We recorded two nests of *M. longicaudatus* with individuals actively transporting nesting material on February 11, 2025. The nests were located behind air conditioning units and their vents (Fig. 3G) on the back walls of two consecutive houses in a periurban residential neighborhood in Manta, Manabí (0°57'S, 80°45'W). The nests were large, composed of numerous twigs, and occupied the space between the air conditioner and the house wall. Mockingbirds from these nests exhibited frequent vocal activity at various times throughout the day. On February 13 2025, both nests were visited by a Shiny Cowbird (*Molothrus bonariensis*) which approached while the mockingbirds were distracted. However, within less than ten seconds, the Shiny Cowbird was chased away by the Mockingbird nest owners.

Saffron Finch (*Sicalis flaveola*):

At least two individuals of *S. flaveola* were documented on the condensing unit of an air conditioner on February 11 2025 in Manta, Manabí along the main avenue of a periurban residential neighborhood

(0°57'S, 80°45'W). The area is characterized by houses with small yards and parks distributed across each block. They were observed in pairs repeatedly entering and exiting the unit (Fig. 3H). During these observations, one individual remained outside, seemingly watching, while the other entered the nest. The nests appeared to be under construction or in the process of maintenance as individuals were seen holding branches in their beaks.

## DISCUSSION

### Nest monitoring and field observations

Nesting behavior in human-made structures was previously reported for *Troglotytes musculus* (León-E et al. 2024), *F. coelestis* (Collar et al. 2020), *M. longicaudatus* (Cody 2020), *P. chalybea* (Turner & Rose 1989), *P. cyanoleuca* (Dayer 2020), *S. flaveola* (Rising et al. 2024), *P. rufocollaris* (Malekan 2020), *F. cinnamomeus* (Kirwan et al. 2023), *Z. auriculata* (Baptista et al. 2024a), *C. cruziana* (Baptista et al. 2024b), and *D. ludovicae* (Stiles et al. 2020). However, this behavior was not previously reported in *C. buckleyi* (Ingels & Greeny 2011, Baptista et al. 2020), *M. micrura* (Schulenberg & Sedgwick 2020), and *T. niveigularis* (Marchant 1960, Cisneros-Heredia 2006, Schulenberg & Johnson 2020). *Amazilia amazilis* has previously nested successfully in captivity which might suggest some flexibility in using artificial structures (Grogan 2000).

Almost all information about the nesting biology of *T. niveigularis* comes from Marchant (1960) who studied this species in southwestern Ecuador. Our nesting records of *T. niveigularis* in Manta during 2024–2025 as well as the presence of this species in the surrounding areas (personal observations) largely agree with the breeding season described for this species: December–June in Peru (Schulenberg et al. 2007) and January–July in Ecuador (Ridgely & Greenfield 2001). Marchant (1960) also recorded nests in southwestern Ecuador in that time range, between February 20 and mid-May (rainy season in Western Ecuador). The nest structure, duration and clutch size also corresponds with previous descriptions: cups of thin twigs and fine fibers, incubation and nesting periods of 15-16 and 14-19 days respectively, and clutch sizes between 2-4 (Schulenberg & Johnson 2020), similar to our observations despite being located on urban infrastructure.

This breeding pair successfully produced three fledglings that completed development and moved to a nearby tree. High success rates have been reported for this species in some years (Marchant data cited by Schulenberg & Johnson 2020), although known interannual variability precludes broad extrapolations. The species is recognized as insectivorous and a berry eater with documented prey of hymenopterans and coleopterans (Taczanowski 1884; Parker data, cited by Hilty & Brown 1986). It has been reported that, in some years, second broods are attempted (Schulenberg & Johnson 2020), as we observed between 2024 and 2025. Our recorded diet included odonates, lepidopterans and tettigonids, expanding the list of prey observed during rearing. The biology of *T. niveigularis* still presents significant gaps especially regarding movement, behavior and habitat use, underscoring the need for more detailed studies in disturbed environments where the species occurs.

The observations of *M. micrura* in Bahía de Caráquez coincide with the reproduction described for that species in Ecuador, reported between March and July following local rains (Marchant 1960, Barrio et al. 2015). Our first nest construction in March 2025 is in this time range. The duration of the observed cycle—approximately one week for construction, 16 days of incubation, and about two weeks of nesting—fits the previously described incubation periods (15–16 days). The nesting phase was shorter than the 22–23 days recorded by Marchant (data cited by Schulenberg & Sedgwick 2020), suggesting a possible effect of being in an area with nearby humans or the artificial substrate used. As is typical for the species, the female was responsible for incubation and parental care (Schulenberg & Sedgwick 2020). The repeated use of the same nest and its placement on a hanging ornament, a previously undocumented substrate, contrasts with traditional nests located in low-lying shrub forks (Alcívar & Cornejo 2022, Barrio et al. 2015). Finally, the abandonment of the second breeding attempt after gardening activities aligns with hummingbirds' high variability in reproductive success and susceptibility to even minor human disturbances (Mendiola-Islas et al. 2023).

The observations made during the first half of 2025 coincided with the rainy season. During this period, a global La Niña Modoki event occurred (Coastal El Niño) characterized by abnormally high temperatures, intense rainfall, and a notable greening of the Ecuadorian coastal strip. These conditions appear to have favored the reproductive activity of several species. The overlap between heavy rainfall and the repeated use of urban infrastructure by *T. niveigularis*, *M. micrura*, and other species whose breeding depends on rain (Marchant 1960) suggests that wet events associated with El Niño–Southern Oscillation climate anomalies can intensify the productivity

and fluctuations in food resources (Grant et al. 2000, Barrantes & Sandoval 2019). These conditions could increase the demand for shelters during nesting and amplify the behavioral plasticity of these birds in environments heavily modified by humans.

### Avifauna in Urban Environments

Our comprehension of avifauna in urban environments is scarce and requires new information about the impacts of urban land use on avifauna. Non-extended examples about biodiversity loss are available for Ecuador. In the capital city, urban green areas of Quito now host 59 bird species compared with previous historical records of around 102 species (Chapman 1926, Montenegro-Pazmiño & Cisneros-Heredia 2015). A study in southern Ecuador (urban and periurban Loja city) found that urbanization significantly affects species diversity with granivorous birds showing some positive responses while insectivorous birds declined mainly due to reduced food availability for this guild (Ordóñez-Delgado et al. 2022). Urban expansion can drive biodiversity loss, however, some species are able to nest in human-made structures (Soldatini et al. 2008, Reynolds et al. 2019).

Some species may choose artificial structures to reduce competition for natural sites (Afrifa et al. 2023), others nest near humans to avoid predators or because these structures provide suitable conditions (Reynolds et al. 2019, Yao et al. 2023). These patterns are documented in some study cases. For example, Southern House Wrens in Brazil nest readily in man-made sites, achieving similar reproductive success in both stable and unstable locations (Alexandrino et al. 2022). In Argentina, Eared Doves use building frameworks for nesting, with reproductive success comparable, though low, to natural sites (Barco et al. 2024). Artificial structures, especially when combined with natural vegetation, might help certain species in urban areas to have successful reproduction (Afrifa et al. 2023). However, there are costs. Nesting in artificial environments can lead to plastic ingestion (Lato et al. 2021, Rangel et al. 2025), increased conflict with humans (Hatch 1996, Araneda et al. 2021), more exposure to dog and cat attacks (Díaz et al. 2023), and behavioral shifts such as reduced anti-predator responses (Møller & Díaz 2018).

Patterns of urban expansion further shape avian communities. In flat landscapes, low-density urban sprawl often creates extensive periurban zones where natural habitats are replaced by human infrastructure (Parés-Ramos et al. 2013). On Ecuador's coast, such land use changes have reshaped ecosystems, negatively impacting wildlife (Dodson & Gentry 1991). Fragmentation can drive rapid biotic homogenization where specialist species disappear and are replaced by widespread generalists—a major contributor to biodiversity loss across large areas (Clavel et al. 2010). Effective conservation in urban settings should maintain patches of native vegetation, create green spaces, and reduce direct human–wildlife conflict. These measures are critical in tropical dry forests, considering their high endemism and vulnerability to habitat loss (Prieto-Torres et al. 2018). Participatory science platforms such as iNaturalist can support urban biodiversity management, offering valuable data to understand the distribution, ecology and behavior of bird species (Callaghan et al. 2022).

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## AUTHOR CONTRIBUTION

All authors conceived the study, designed the methodology, collected the data, curated the records, interpreted the results and wrote the manuscript. DVC, EVB and AGC conducted the analyses and prepared the figures. All authors approved the final version and agreed to be accountable for its contents.

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# NEST-SITE CHARACTERISTICS OF RUFOUS HORNERO (*Furnarius rufus*) ACROSS ITS DISTRIBUTION AS REPORTED BY CITIZEN SCIENTISTS

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**ABSTRACT:** Nests provide a secure place for eggs and offspring, offer camouflage and defense against predators, and can also help moderate the microenvironment. Although most nests serve similar functions, nest traits can vary widely across and within species. While nest architecture is largely constrained by genetics, nest-site characteristics are more strongly shaped by external factors and are therefore expected to vary with environmental conditions. Yet most evidence for this pattern comes from comparative studies across species, while large-scale spatial variation within species remains understudied. Here, we described the nest-site characteristics of 13,325 Rufous Hornero nests (*Furnarius rufus*) reported by citizen scientists across the species' entire distribution. We characterized nest height, nest substrate type (natural *vs* artificial), and nest cover (covered *vs* uncovered) across urban, rural, and natural areas. We also examined how nest height and nest cover varied along latitudinal and longitudinal gradients within each environment, as well as the relationship between nest cover and nest height across these three environmental contexts. We found that nest height tended to be similar in natural, rural, and urban areas; that horneros in rural and urban areas more frequently built nests on artificial substrates, whereas nests in natural areas were more often built on natural substrates; that uncovered nests were more common in urban and rural areas, while in natural areas covered and uncovered nests occurred in similar proportions; that nest height and cover varied geographically, especially for rural and urban populations; and that, regardless of environmental context, higher nests and nests built on artificial substrates were more likely to be uncovered than those closer to the ground or built on natural substrates. Overall, our results show that horneros exhibit substantial flexibility in nest-site characteristics across environments, raising questions about whether this variation reflects nest-site preferences, availability of breeding sites, or both.

**KEYWORDS:** *breeding, domed nests, Furnariidae, nesting biology, suboscine*

Most bird species use nests (Fang et al. 2018). Nests provide a secure substrate for eggs and offspring, offer camouflage and defense against predators, and help moderate the microenvironment (e.g., temperature; Collias & Collias 1986). Although most nests serve similar functions, nest characteristics can vary substantially across and within species and potentially influence individual reproductive success (Hansell 2000, reviewed by Mainwaring et al. 2014). However, in comparison with other aspects of avian research, we know little about nesting biology in birds (Deeming & Reynolds 2016, Mainwaring et al. 2016, Perez et al. 2023), partly because of the long-standing view of nest building as an instinctive and inflexible behavior (Guillette & Healy 2015, Healy et al. 2023).

Compared to nest architecture, which is subject to strong genetic constraints, nest site characteristics are more frequently influenced by external factors (Fang et al. 2018), such as the availability of nesting sites, predation risk, and climate, among others (Collias & Collias 1986, Hansell 2005, Martin et al. 2017). For example, nesting sites in urban locations include

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both natural (i.e., native and non-native vegetation) and artificial (i.e., anthropogenic structures) opportunities, whereas natural areas tend to provide only natural nesting opportunities (reviewed by Reynold et al. 2019). Likewise, nest height is expected to relate to predation risk and human disturbance with higher nests thought to be less accessible to ground predators and/or pedestrians (e.g., Wang et al. 2008, Becker & Weisberg 2014, reviewed by Sheard et al. 2024), while nest cover is expected to influence concealment from aerial predators (discussed by Jara et al. 2020). Additionally, because temperature can strongly influence embryonic viability, bird nests are predicted to adjust to sun exposure according to geographic location (reviewed by Mainwaring et al. 2016). In temperate environments, nests are often placed in sites that warm more quickly and retain heat longer than those in tropical environments (reviewed by Mainwaring et al. 2016). Consequently, nest characteristics are expected to vary adaptively in response to predictable environmental conditions. However, most evidence supporting this idea comes from comparative studies across species (reviewed by Mainwaring 2017). Large-scale spatial variation within species is less frequently explored. Few studies focus on a single species to provide a comprehensive understanding of variation in nest-building behavior (reviewed by Mainwaring 2017). Exceptions include studies of the House Sparrow (*Passer domesticus*), Blue Tit (*Cyanistes caeruleus*), and Great Tit (*Parus major*). These cavity-nesting species are widely studied across Europe and exhibit substantial variation in nesting characteristics. They breed in natural, rural, and urban environments, use natural (e.g., wood cavities) and artificial structures (e.g., concrete nest boxes, pipes), and select nest sites based on the presence or absence of conspecifics and heterospecifics, among other factors (House Sparrow: e.g., Indykiewicz 1991; Blue and Great tits: reviewed by Mainwaring 2017). While this information is highly valuable, it primarily reflects the nesting characteristics of species that rely on pre-existing cavities, mainly nest boxes provided by researchers. Consequently, we lack data on nest site characteristics of species that build their own cavities. Studies examining the range-wide variation in nest site properties in these species are needed to better understand how birds adapt their building behaviors to current environmental conditions.

Furnaridae, also known as ovenbirds, is a diverse family of small to medium-size suboscine birds found in the Neotropics (Winkler et al. 2020). Ovenbirds build a diversity of nest types including complex domed nests (Winkler et al. 2020), which have been identified as the ancestral nest type among passerine birds (reviewed by Mainwaring et al. 2023). In particular, the Rufous Hornero (*Furnarius rufus*; hereafter Hornero) is widely distributed across natural, rural, and urban areas in Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Remsen & Bonan 2020). Horneros commonly breed in open and semi-open habitats such as grasslands, savannas, pastures, agricultural fields, roadsides, gardens, and urban environments (Remsen & Bonan 2020). Nests are constructed by males and females of mud, straw and animal feces (Fig. 1; Fraga 1980, Massoni et al. 2012). Most individuals construct a new nest each breeding season, often near previous nests, consistent with strong year-round territoriality and the persistence of old nests for several years (Fraga 1980). Nest construction typically begins at least two to three months before egg laying (e.g., Fraga 1980), although its duration varies substantially among pairs (the building process may last from 8–14 days to several months; unpubl. data). Old Hornero nests can last for several years and be used by other animals (reviewed by Mentesana et al. 2024). Nest predators include raptors (Chimango Caracara, *Daptrius chimango*; Black-chested Buzzard-Eagle, *Geranoaetus melanoleucus*; Roadside Hawk, *Rupornis magnirostris*; Crested Caracara, *Caracara plancus*), mammals (White-eared Opossum, *Didelphis albiventris*; domestic cat, *Felis catus* —the latter also preys on adults away from nests), and snakes (e.g., Philodryas patagoniensis; Fraga 1980, Mason 1985, Salvador 2016, Garreta & Rivas-Ortiz 2026, WikiAves 2026). Despite the species' broad distribution, the only information regarding nest site properties of the Hornero comes from two studies. Mason (1985) reported a mean nest height of 2.6 ± 1.2 m (range: 1.2 – 4.9 m) for 17 nests found in two rural areas of Buenos Aires Province, Argentina, and Schaaf et al. (2018) reported that Hornero nests located at lower latitudes (e.g., San Salvador de Jujuy Province, Argentina) tended to be covered compared to nests located at higher latitudes (e.g., La Plata City, Buenos Aires Province, Argentina). However, because individuals can choose where to build their nests across a broad range of environments, horneros are expected to exhibit considerable flexibility in nest height and other nest site characteristics.

Quantifying variation in nest traits across the entire distribution of a species is a challenging task. One way to address this task is by involving the public in scientific research. This collective approach, known as citizen science, offers the major advantage of

generating large amounts of data across broad spatial scales. In ornithology, citizen science initiatives are widely used to identify bird species (e.g., iNaturalist 2025), record real-time sightings that improve our understanding of migration patterns and species distributions (eBird: Sullivan et al. 2009), document bird–window collisions (reviewed by Loss et al. 2023), and collect nesting records of numerous species (e.g., NestWatch, Cornell Lab of Ornithology: Bailey et al. 2024), among others.

In this descriptive study, we characterize Hornero nest-site characteristics across its entire distribution using a citizen science approach. This approach allowed us to characterize (1) nest substrate type (i.e., whether the nest was built on natural or artificial, human-made structures; Fig. 1A), (2) nest height (i.e., meters above the ground), and (3) nest cover (i.e., whether the nest was protected or not by either a natural or artificial structure; Fig. 1B) across urban, rural, and natural areas. We also examined how nest height and nest cover varied along latitudinal and longitudinal gradients within each type of environment (i.e., rural, urban, natural). These two geographic variables are strongly correlated with abiotic factors such as temperature, precipitation, wind, and elevation: from southern Brazil to central and southern Argentina, temperatures generally decrease, precipitation progressively declines, and wind intensity generally increases. Also, elevation shifts from lowland coastal and plain regions in Brazil, Uruguay, and eastern Argentina to the high Andes of western Argentina and Bolivia. During the Hornero breeding season, this elevational gradient is associated with warmer temperatures, lower precipitation, and generally weaker winds in mountainous regions. Lastly, we examined the relationships between (4) nest cover and nest height and (5) nest cover and substrate type for nests reported across these three environmental contexts. While acknowledging the descriptive nature of our study, we defined five guiding predictions to structure our analyses and interpret the results. First, we predicted that nests in natural areas would be built mainly on natural structures compared to those in rural and urban areas, because suitable nesting sites are scarcer in cities (reviewed by Reynolds et al. 2019). We also expected nests in rural areas to be built on more natural substrates than those in urban areas, as natural substrates are probably more common in rural settings. Second, we predicted nest height to be lower in natural and rural areas than in urban areas because higher nests are thought to be less accessible to ground predators (e.g., cats) and/or pedestrians (Jara et al. 2020), and nest detection by predators generally decreases with increasing urbanization (meta-analysis by Vincze et al. 2017). We also predicted that to reduce sun exposure, nests at lower latitudes (i.e., closer to the Equator) and higher longitudes (i.e., toward the Andes) would be built at lower heights than nests at higher latitudes and lower longitudes. Third, if nest cover reflects behavioral adaptations of horneros to avoid predation and/or harsh weather conditions, we predicted the majority of nests to be covered across the three environmental contexts. Moreover, Hornero nests located closer to the Equator tended to be found in areas with more vegetation cover (Schaaf et al. 2018). Therefore, we predicted nests at lower latitudes and higher longitudes to be more frequently covered than those at higher latitudes and lower longitudes. Fourth, if nest cover provides better nest concealment from aerial predators (discussed by Jara et al. 2020), we predicted higher nests would have more cover than nests located at lower heights. We predicted no differences in this relationship across natural, rural and urban areas. Finally, we predicted uncovered nests to be mainly built on artificial structures.

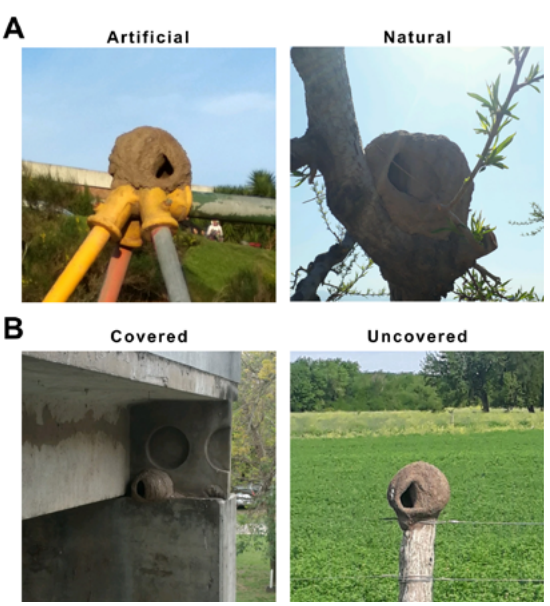


**Figure 1.** Examples of two Hornero (*Furnarius rufus*) nest site characteristics reported by citizen scientists across natural, rural and urban areas in Argentina, Bolivia, Brazil, Paraguay, and Uruguay: (A) nest substrate type (i.e., if the nest was built on a natural or artificial, human-made structure), and (B) nest cover (i.e., whether the nest was covered or not by either a natural or artificial structure). Pictures were sent by citizen scientists via a smartphone application.

## MATERIALS AND METHODS

### Data collection

We collected data from 13,325 nests throughout the species' range during October 2018 to October 2019. Using a free smartphone application developed in Spanish and Portuguese, 1300 citizen scientists from Argentina, Bolivia, Brazil, Paraguay, and Uruguay collected data on Hornero nests. The application consisted of an eight-step process whereby users answered multiple-choice questions *in situ* each time they encountered a nest. The questions were carefully designed to ensure unequivocal interpretation and were accompanied by guiding schemes when necessary. For this study, we used data reported on four nest-site properties: environmental context (i.e., urban — small and large cities; rural — areas with agroindustrial and agroecosystem production; or natural — areas not modified by humans), substrate, height, and cover. Based on nest GPS locations, we also gathered geographic information such as latitude (min- max range: -10.281, -43.405) and longitude (min-max range: -37.284, -69.407). For more details on data curation and validation see Adreani et al. 2022, 2025.

From a previous study, only 3.8% of the reported nests were closer than 25 m to another reported nest, indicating that if pseudo-replication occurred by several users reporting the same nest or users reporting several nests from the same Hornero pair, this effect was minimal (see also Adreani et. al., 2022).

### Data analyses

We determined the number of nests built on artificial and natural substrates, the number of uncovered and covered nests, and calculated the mean and standard deviation (mean ± SD) of nest height across urban, rural, and natural environments.

We tested whether nest characteristics differed significantly among environmental contexts. First, to test for differences in the substrate used for nest construction across contexts, we created a generalized linear mixed-effects model with a binomial distribution, using nest substrate (levels: natural, artificial) as the response variable, environmental context as a fixed factor, and user ID as a random factor. Second, to test for differences in nest height among natural, rural and urban areas across latitudinal and longitudinal gradients, we created a linear mixed-effects model with nest height as the response variable, environmental context (levels: urban, rural, natural) as a fixed factor, scaled latitude and scaled longitude as covariates, their interaction, the interaction between environmental context and both latitude and longitude, and user ID as a random factor. Third, to test for differences in nest cover across contexts along latitudinal and altitudinal gradients, we created another generalized linear mixed-effects model, with binomial distribution, with nest cover (levels: yes, no) as the response variable, environmental context as a fixed factor, scaled latitude and scaled longitude as covariates, their interaction, the interaction between environmental context and both latitude and longitude, and user ID as a random factor. Four, to test for the relationship between nest cover and nest height across these three environmental contexts, we created a generalized linear mixed-effects model, with binomial distribution, with nest cover as the response variable, nest height as a covariate, environmental context as a fixed factor, their interaction, and user ID as a random factor. Finally, to test for the relationship between nest cover and nest substrate across these three environmental contexts, we created a generalized linear mixed-effects model, with binomial distribution, with nest cover as the response variable, nest substrate as a fixed factor, environmental context as a fixed factor, their interaction, and user ID as a random factor.

We performed all analyses in R v.4.3.2 (R Core Team 2021) with the packages '*lme4*' (Bates et al. 2015) and '*arm*' (Gelman & Yu-Sung 2015) using a pseudo-Bayesian framework with non-informative priors (Korner-Nievergelt et al. 2015). We verified linear model assumptions by inspecting residual plots using the package '*DHARMa*' (Hartig 2024). We used the '*sim*' function to simulate posterior distributions, extracting mean estimates, 95% credible intervals, and posterior probabilities from 10,000 simulations (Gelman & Hill 2007). Following Korner-Nievergelt et al. (2015) we considered effects to be statistically meaningful when zero was not included in the 95% credible intervals.

## RESULTS

From the 13,325 nest reports to our database, 7667 nests were in urban areas, 5138 in rural areas, and 520 in natural areas.

### Nest site substrate

Most Hornero nests were built on artificial substrates ($n$ = 7566) rather than on natural substrates ($n$ = 5751). When examining substrates in relation to the type of area where the nests were reported, Horneros in rural and urban areas built more nests on artificial substrates than on natural ones (Fig. 2, Table 1; rural: $n_{artificial}$ = 3364, $n_{natural}$ = 1774; urban: $n_{artificial}$ = 4095,

$n_{natural}$ = 3566). The two locations did not differ in the nest site substrate ($p$-value = 0.080). In natural areas, by contrast, Hornero nests were more likely to be found on natural substrates (Fig. 2, Table 1; natural: $n_{artificial}$ = 107, $n_{natural}$ = 411).

### Nest height

Across its distribution, Hornero nests were found from sea level (i.e., 4.11 m.s.m.n; e.g., in La Paloma, Rocha, Uruguay) to approximately 2895.75 m.s.n.m in Sucre, Bolivia (see data in Mentesana & Adreani 2026). Regardless of altitude, the overall mean nest height (± SD) was 6.669 ± 2.482 m (min-max range: 0 – 15 m). Nest height was statistically different between nests located in urban, rural, and natural areas (Fig. 3A, Table 2; mean ± SD: 6.836 ± 2.542 m, 6.482 ± 2.341 m, and 6.054 ± 2.694 m, respectively); yet the effect sizes of these differences were small.

In rural and urban areas but not in natural ones, nests closer to the Equator were located lower than nests further south (posterior probabilities: natural = 0.866, rural = 1, urban = 0.992; Fig. 3B, Table 2). Additionally, only in rural areas but not in natural or urban areas, nests closer to the Andes (i.e., to the west) tended to be higher than those located farther east (posterior probabilities: natural = 0.616, rural = 0.977, urban = 0.127; Fig. 3C, Table 2).

### Nest cover

Most Hornero nests were not covered ($n_{not\ covered}$ = 8459; $n_{covered}$ = 4866). When examining nest cover in relation to the type of area where the nests were reported, uncovered nests were more likely to be found in rural and urban areas (Fig. 4A, Table 2; rural: $n_{not\ covered}$ = 3920; $n_{covered}$ = 1218; urban: $n_{not\ covered}$ = 4279; $n_{covered}$ = 3388). However, in natural areas, uncovered and covered nests were equally represented (Fig. 4A, Table 2; $n_{not\ covered}$ = 260; $n_{covered}$ = 260).

In the three areas, nests located closer to the Equator tended to be uncovered compared to nests located farther south (posterior probabilities: natural = 0.997, rural = 0.996, urban = 0.967; Fig. 4B, Table 2), whereas in rural and urban areas but not in natural areas, nests located closer to the Andes tended to be more frequently covered (posterior probabilities: natural = 0.078, rural = 0.981, urban = 0.999; Fig. 4C, Table 2).

### Nest cover in relation to nest height

Higher nests were more likely to be uncovered in the three environmental contexts (Fig. 5A, Table 3).

### Nest cover in relation to nest substrate type

Across natural, rural, and urban areas, nests on artificial substrates were more often uncovered while nests on natural substrates were more often covered (Fig. 5B, Table 3).

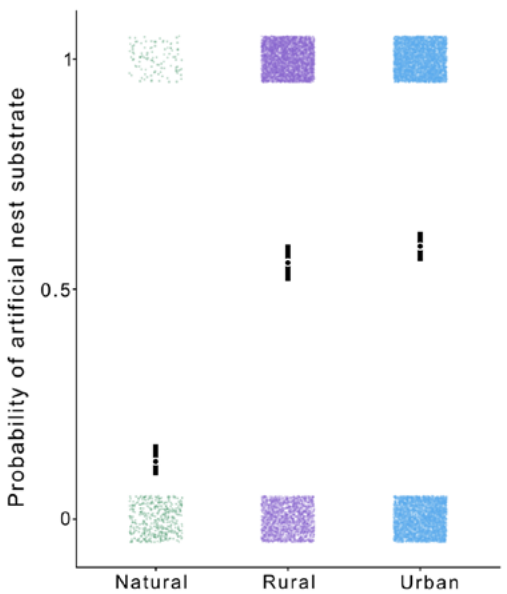


**Figure 2.** Nest site substrate (0 = if built on a natural structure; 1 = if built on an artificial, human-made structure) of horneros (*Furnarius rufus*) reported by citizen scientists across natural, rural, and urban areas in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Colored dots represent the raw data for natural (green), rural (purple) and urban (blue) contexts. Black dots and vertical bars represent model estimates and 95% credible intervals, respectively.

**Table 1.** Results of a generalized linear mixed effect model testing nest site substrate (i.e., whether the nests were built on natural or artificial, human-made structures) of horneros (*Furnarius rufus*) across urban, rural and natural areas, respectively. The data used in each model correspond to nest-site characteristics reported by citizen scientists across Argentina, Bolivia, Brazil, Paraguay, and Uruguay.

| | **Nest site substrate** |
|---|---|
| **Fixed effects** β | |
| Intercept (*Natural*) | -1.943 (-2.246; -1.642) |
| Rural | 2.175 (1.879; 2.472) |
| Urban | 2.320 (2.021; 2.609) |
| **Random effects** $\sigma^2$ | |
| User ID | 2.727 (2.549; 2.909) |

## DISCUSSION

We described three nest-site properties of the Hornero across its entire distribution using a citizen science approach (Table 4). Our results suggest that horneros exhibit considerable flexibility in nest substrate, height, and cover across natural, rural and urban environmental contexts, and that nest height and cover also vary along latitudinal and longitudinal gradients. A common characteristic across the three environmental contexts was that nests located high up and nests built on artificial structures tended to be uncovered compared to nests located lower and built on natural structures.

A natural question arising from our results is the extent to which the observed flexibility in nest-site properties across natural, rural, and urban contexts reflects true preferences of horneros for specific nest-site characteristics. Such preferences might be a consequence of horneros experiencing different types of selection pressures. For example, Hornero nest height might be a trait shaped by the presence of aerial and ground predators and/or human disturbance, each of which might differ in their influence across natural, rural and urban areas. Although nest height was lower in natural and rural areas compared to urban ones, these differences—while statistically significant—were less than one meter. Biologically, these results suggest that nest height is comparable across environmental contexts and considerably higher than the only previously published studies from two rural areas in Argentina (Mason 1985). Consistent with the idea that horneros prefer a specific nest height, this trait was similar across areas even though nests were built on different substrates (i.e., in natural habitats, most nests were built on natural substrates unlike rural and urban sites). Nest-site characteristics might also reflect active choices by horneros to cope with environmental variation. In fact, for the enclosed nests built by horneros every year, thermal benefits are predicted to be an important factor shaping the evolution of these structures (reviewed by Martin et al. 2017). Nests at lower latitudes and higher longitudes, where sun exposure is expected to be greater, were built lower than those at higher latitudes and lower longitudes. However, we observed the opposite trend for nest cover with nests closer to the Equator being mainly uncovered. These results suggest that, in addition to temperature, other environmental factors (e.g., wind and precipitation) may also influence nest-site choice.

Alternatively, and not mutually exclusive, nest-site characteristics might reflect differences in nest-site

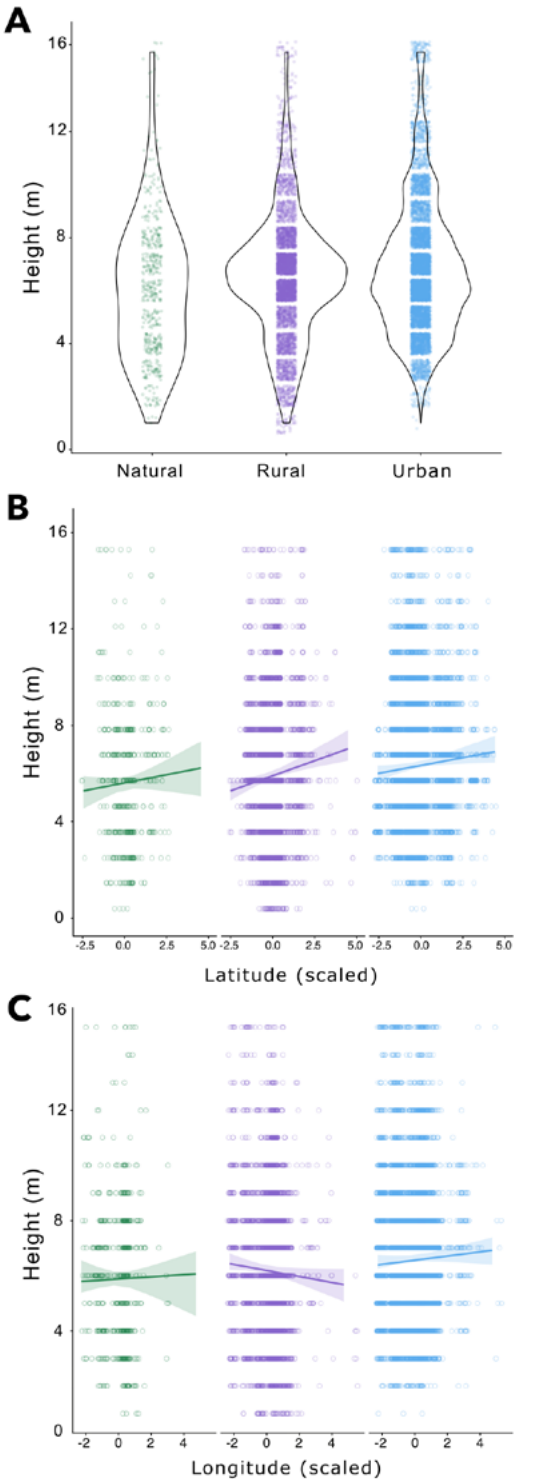


**Figure 3.** Nest height (i.e., meters of the nest above the ground) of horneros (*Furnarius rufus*) reported by citizen scientists across natural, rural, and urban areas in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Colored dots represent the raw data for natural (green), rural (purple) and urban (blue) contexts. Model mean estimates are represented with black dots (A) and colored lines (B & C), and 95% credible intervals are represented with vertical bars (A) and colored shades (B & C).

availability across areas. For example, across natural, rural, and urban environments, nests lacking overhead protection were mainly found at greater heights above the ground. This relationship might result from the abundance of human-made structures (e.g., light or electrical poles), which are widely used by horneros for breeding (pers. obs.), rather than representing a behavioral adaptation against predators or environmental variation (e.g., Jara et al. 2020). Supporting this idea, uncovered nests were also associated with nests built on artificial structures. Moreover, Hornero nest site characteristics might also reflect behavioral and ecological factors operating outside the breeding season. Horneros are territorial year-round and pairs remain together in the same territory across years (Fraga 1980, Diniz et al. 2019, Mentesana et al. 2020).

**Table 2.** Results of a univariate mixed model and a generalized linear mixed effect model testing nest height (i.e., meters above the ground) and nest cover (i.e., whether the nests were covered by natural or artificial structures) of horneros (*Furnarius rufus*) across a latitudinal and longitudinal gradient from urban, rural and natural areas. The data used in each model correspond to nest-site characteristics reported by citizen scientists across Argentina, Bolivia, Brazil, Paraguay, and Uruguay.

| | **Nest Height** | **Nest Cover** |
|---|---|---|
| | **Fixed effects β (95% CrI)** | |
| Intercept (*Natural*) | 5.881 (5.647; 6.117) | -0.116 (-0.384; 0.149) |
| Rural | 0.348 (0.119; 0.574) | 0.958 (0.702; 1.215) |
| Urban | 0.747 (0.518; 0.974) | 0.640 (0.381; 0.897) |
| Scaled Latitude | 0.134 (-0.104; 0.372) | -0.400 (-0.692; -0.111) |
| Scaled Longitude | -0.034 (-0.283; 0.209) | -0.194 (-0.464; 0.076) |
| Rural * Scaled Latitude | 0.120 (-0.115; 0.358) | 0.198 (-0.099; 0.498) |
| Urban * Scaled Latitude | 0.001 (-0.231; 0.235) | 0.288 (0.001; 0.579) |
| Rural * Scaled Longitude | -0.088 (-0.335; 0.163) | 0.336 (0.060; 0.616) |
| Urban * Scaled Longitude | 0.091 (-0.150; 0.333) | 0.383 (0.108; 0.650) |
| Scaled Latitude * Scaled Longitude | 0.006 (-0.052; 0.063) | -0.019 (-0.085; 0.047) |
| | **Random effects $\sigma^2$ (95% CrI)** | |
| User ID | 2.808 (2.641; 2.978) | 2.904 (2.720; 3.098) |
| Residual | 4.340 (4.235; 4.445) | - |

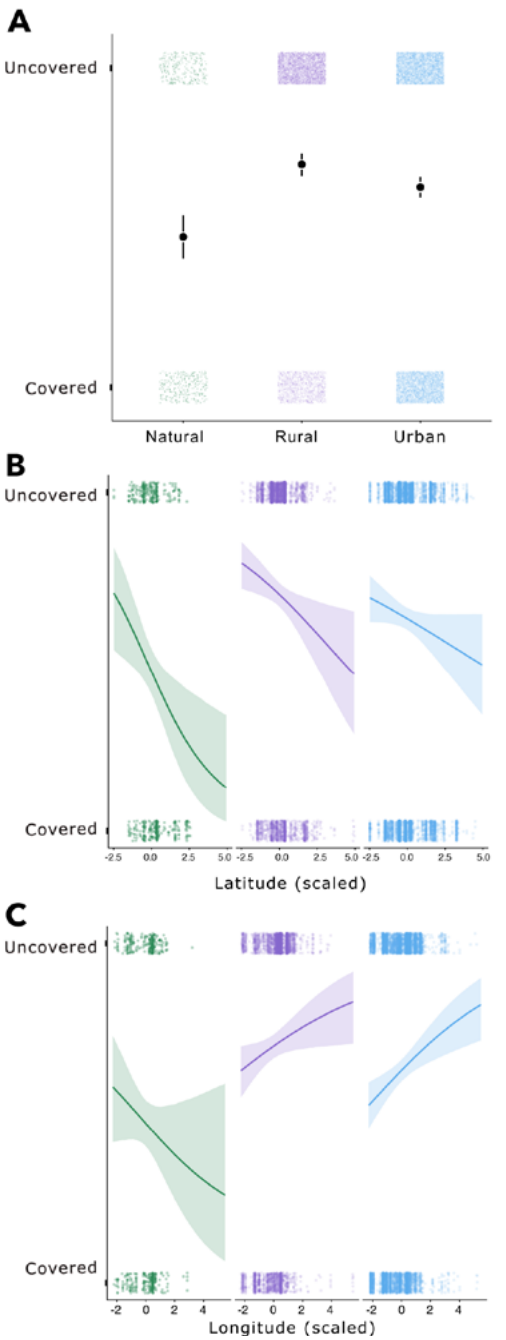


**Figure 4.** Nest cover (i.e., whether the nest was covered or not by either a natural or artificial structure) of horneros (*Furnarius rufus*) reported by citizen scientists across natural, rural, and urban areas in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Colored dots represent the raw data for natural (green), rural (purple) and urban (blue) contexts. Model mean estimates are represented with black dots (A) and colored lines (B & C), and 95% credible intervals are represented with vertical bars (A) and colored shades (B & C).

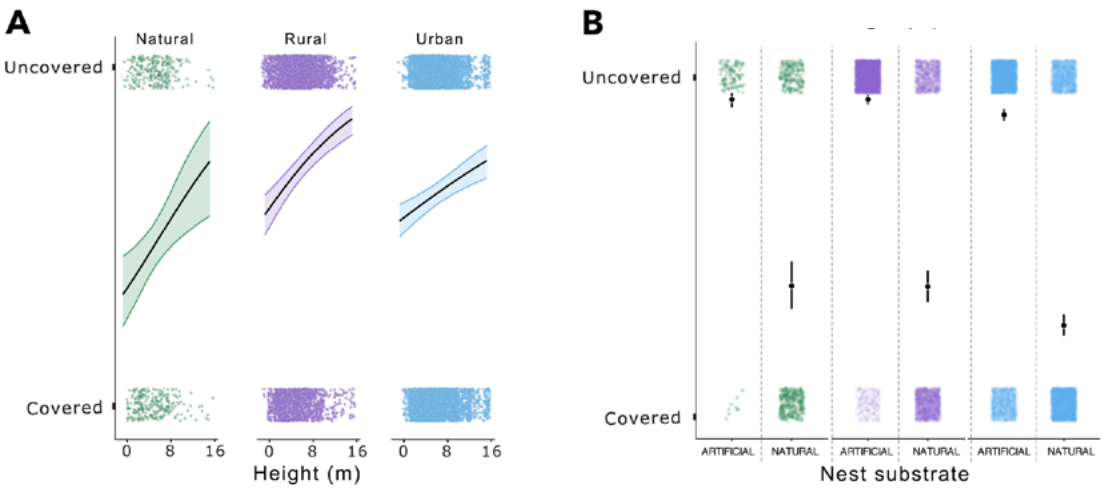


**Figure 5.** Relationship between Hornero (*Furnarius rufus*) (A) nest height (i.e., meters of the nest above the ground) and (B) nest substrate (0 = if built on a natural structure; 1 = if built on an artificial, human-made structure) with the probability of nest cover (i.e., whether the nest was covered or not by either a natural or artificial structure) reported by citizen scientists across natural, rural, and urban areas in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Grey dots represent raw data. Black lines represent model mean estimates and colored shades (A) and vertical bars (B) show the 95% credible intervals for natural (green), rural (purple) and urban (blue) environmental contexts.

**Table 3.** Results of two generalized linear mixed effect models testing nest cover (i.e., whether the nests were covered or not by natural or artificial structures) of horneros (*Furnarius rufus*) in relation to nest height and nest site substrate (i.e., if the nests were built on natural or artificial, human-made structures), respectively, across urban, rural and natural areas. The data used in each model correspond to nest-site characteristics reported by citizen scientists across Argentina, Bolivia, Brazil, Paraguay, and Uruguay.

| **Nest Cover** | | **Nest Cover** | |
|---|---|---|---|
| **Fixed effects β (95% CrI)** | | **Fixed effects β (95% CrI)** | |
| Intercept (Natural) | -0.825 (-1.378; -0.268) | Intercept (Natural) | -0.570 (-0.884; -0.256) |
| Rural | 1.007 (0.424; 1.600) | Rural | -0.001 (-0.314; 0.294) |
| Urban | 0.981 (0.401; 1.562) | Urban | -0.574 (-0.872; -0.270) |
| Height | 0.122 (0.043; 0.203) | Nest site substrate | 3.176 (3.046; 3.306) |
| Rural * Height | -0.013 (-0.101; 0.074) | | |
| Urban * Height | -0.065 (-0.145; 0.018) | | |
| **Random effects $\sigma^2$ (95% CrI)** | | **Random effects $\sigma^2$ (95% CrI)** | |
| User ID | 3.119 (2.919; 3.329) | User ID | 4.411 (4.135; 4.708) |

Thus, securing a high-quality territory that provides food year-round may be the main factor driving territory settlement while nest site characteristics simply reflect the nesting options available within that territory. An approach towards determining the extent to which the observed flexibility in nest-site characteristics reflects Hornero preference, breeding-site availability, or both would quantify nest-site availability and compare it with observed Hornero nest-site selection. A second, and complementary, approach would quantify the relationship between nest site characteristics and reproductive success across locations. With this information, a third study could experimentally manipulate individual nest site characteristics and combined traits to gain a full understanding of the evolutionary forces acting on Hornero nest site choice.

Besides ecological and behavioral factors, our results may be influenced by the data collection methodology. Although the citizen science approach enables broad spatial coverage and large sample sizes, the conspicuousness of Hornero nests, particularly in open areas, may introduce reporting biases. For example, participants may been more likely to report uncovered nests and/or nests on artificial substrates. Similarly, some nest traits might be influenced by the date when citizen scientists recorded the nest. For example, nest cover might be reported differently if the nest was located beneath trees whose leaf phenology varies seasonally. While plausible, we believe these factors did not strongly influence our results given that nest cover can result from both natural and artificial structures and the models exploring this trait yielded strong effects. To disentangle true nest-site characteristic preferences from potential sampling bias, future studies could employ structured designs based on random or stratified-random samples.

Hornero nest site characteristics might influence the reproductive success of other animals with broad implications for ecosystem dynamics. Most horneros build a new nest every season and old nests are used by secondary cavity-nesting birds, mammals and invertebrates (reviewed by Mentesana et al. 2024). A survey of the literature reveals that Hornero nests are used by at least 29 bird species from 13 families, mostly in the order Passeriformes (Delhey 2018). Our results suggest that the widespread use of Hornero nests by other species may stem from the diversity of nest sites that horneros provide across and within environmental contexts. Likewise, these nest sites might act as ecological traps for some species by

**Table 4.** Summary of the nest-site characteristics described for the Hornero (*Rufous Hornero*) in relation to different variables expected to influence them including our predictions and the results obtained. Symbols indicate relative magnitude or similarity among categories (e.g., Natural < Rural < Urban; Natural ≈ Rural ≈ Urban). 'Closer to the Equator' refers to lower latitudes, whereas 'closer to the Andes' refers to higher longitudes within the study region (Argentina, Bolivia, Brazil, Paraguay, and Uruguay).

| | In relation to | Predictions | Results found in this study |
|---|---|---|---|
| Nest site substrate | Environmental context | Natural substrates: Natural > Rural > Urban | Natural areas: mostly natural substrates; rural/urban areas: mostly artificial substrates |
| Nest height | Environmental context | Natural < Rural < Urban | Natural ≈ Rural ≈ Urban |
| | Environmental context & Geographic location | Lower closer to the Equator and Andes | In rural/urban areas, nests closer to the Equator were lower; in rural areas, nests closer to the Andes were higher |
| Nest cover | Environmental context | Most nests covered | Natural areas: covered and uncovered nests equally common; rural/urban areas: mostly uncovered |
| | Environmental context & Geographic location | Greater cover closer to the Equator and Andes | Closer to the Equator: less covered; closer to the Andes: more covered (rural/urban only) |
| Nest cover | Environmental context & Nest height | Higher nests more covered | Higher nests more often uncovered |
| Nest cover | Environmental context & Nest substrate type | Nests on artificial substrates less covered than natural substrates | Nests on artificial substrates were more often uncovered |

negatively affecting productivity, fledgling or adult survival, nestling condition, and/or brood parasitism rates (reviewed by Reynolds et al. 2019). These negative effects might occur because breeding passerines typically forage close to their nests making nest-site characteristics influential in determining food availability for nestlings, because nests on human-made structures might only be temporarily available, or because they might occur in areas with high competition or parasitism, among other factors. To the best of our knowledge, no studies have investigated the implications of Hornero nest site characteristics on the breeding success of other bird species nor whether any advantages or disadvantages associated with these nests vary across natural, rural, or urban contexts.

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## AUTHOR CONTRIBUTION

Conceptualization: LM and NMA. Methodology: LM, and NMA. Software: LM and NMA. Validation: MNA. Formal Analysis: LM and NMA. Investigation: LM and NMA. Resources: LM and NMA. Data curation: MNA. Writing – original draft: LM. Writing – review & editing: LM and NMA. Visualization: NMA. Supervision: LM and NMA. Project administration: LM and NMA. Funding acquisition: LM and NMA.

## DATA AVAILABILITY STATEMENT

All data and code are available at Zenodo (Mentesana & Adreani 2026).

## SUPPLEMENTARY MATERIAL

You can access the supplementary material for this article by visiting the link: https://doi.org/10.56178/eh.v41i1.1540.

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# THE AVIFAUNA IN THE DIFFERENT LANDSCAPE COMPONENTS OF ARROYO SALADILLO, SOUTHERN SANTA FE PROVINCE, ARGENTINA

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**ABSTRACT:** In this study, we estimated and compared patterns of biodiversity of avifauna in the different landscape units that make up the middle basin of the Arroyo Saladillo, located in Santa Fe Province, Argentina. We found that species richness, abundance, and diversity were higher in the corridor than in the rest of the landscape units, with the simplified matrix showing the lowest values. The low-simplification matrix and patches showed similar values for the parameters analyzed. In addition, we analyzed avifauna abundance, richness, and diversity across different seasons and their relationship with the landscape units under study. We observed that richness, abundance, and diversity of wild birds were significantly higher during spring and summer compared to other seasons, with simplified matrix areas recording the lowest values for these indicators. Biological corridors and patches showed similar seasonal variability. The low-simplification matrix showed patterns of seasonal variability similar to those observed in patches. These results highlight the importance of biological corridors and relict areas with high diversity of woody plant species, which act as biodiversity islands. In addition, it is important to consider the role played by productive fields with a low degree of simplification as key habitats for the conservation of wild birds. We consider it essential to preserve this type of production in the region and to encourage the implementation of diversified production systems, since they play a fundamental role in the conservation of wildlife in the region.

**KEYWORDS:** *biodiversity, birds, landscape ecology, Pampas region*

Species diversity is a central topic in both community ecology and conservation biology (Villarreal et al. 2004). Its study has gained increasing relevance in recent years due to the modifications generated by human activities (Sala et al. 2000, Wilson et al. 2016).

In the Pampas region, agricultural expansion and population growth are key factors driving environmental transformation (Brown et al. 2006). Agricultural intensification has been mainly expressed through the expansion of double-cropping wheat–soybean systems, the widespread adoption of no-till farming, and the incorporation of transgenic cultivars (Aizen et al. 2009). These processes have drastically reduced natural environments and altered ecosystem structure and functioning, leading to fragmentation (Rimoldi & Chimento 2018). As a consequence, landscapes have become increasingly homogeneous, a condition identified as one of the main drivers of the decline of numerous vertebrate groups in temperate agroecosystems (Benton et al. 2003).

In this scenario, wildlife faces increasing threats due to habitat loss and fragmentation (IUCN 2008). The sensitivity of species to these alterations depends on their spatial requirements, diets, and behavioral responses to landscape change (Biasatti & Rimoldi 2022). Among the most affected groups, birds stand out for their ability to respond rapidly to environmental modifications at both regional and local scales,

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moving in response to resource variation or abandoning areas where resources are no longer available (Robinson et al. 2004, Guidetti 2020). However, these responses vary among species or assemblages, making birds valuable indicators for understanding ecosystem condition (Whelan et al. 2008, Wenny et al. 2011, Zufiaurre et al. 2016).

Beyond their role as bioindicators (BirdLife International 2022), birds perform key ecosystem functions with direct effects on human well-being, such as pollination (Murphy & Kelly 2001), regulation of invertebrate populations (Mols & Visser 2002), natural rodent control (Rimoldi & Curti 2021), and seed dispersal (Guidetti 2020).

At the landscape level, the distribution, abundance, and composition of bird communities are closely linked to land-use patterns, which determine habitat availability and quality (Allen & O'Connor 2000, Heikkinen et al. 2004, La Sorte 2006, Codesido & Busch 2010). Thus, environmental degradation can be assessed through changes in density, abundance, and distribution of populations across the different environments resulting from land-use patterns (Temple & Wiens 1989).

The impacts of intensive agriculture are not limited to habitat loss: the intensive use of pesticides and agrochemicals affects beneficial species, reducing biodiversity and weakening essential ecosystem services (Krüger 2013). However, certain well-managed agroecosystems can retain a considerable portion of their original biodiversity (Mermoz et al. 2016).

Both seasonal variation and anthropogenic land-use changes affect bird community dynamics. Seasonal changes in climate and food resource availability influence habitat use, causing fluctuations in richness, abundance, and composition (Codesido et al. 2004, López de Casenave et al. 2008, Evans et al. 2013). However, changes driven by rapid and extensive land-use transformation are often more pronounced, as they affect both species distribution and relative abundance across habitats, as well as the resources available to different functional groups (Zanette et al. 2000, Silva 2003).

In this context, the objective of this study was to compare bird assemblages among the different landscape components present in the middle basin of the Arroyo Saladillo (southern Santa Fe Province, Argentina). Specifically, we evaluated differences in richness, abundance, and diversity. Additionally, we assessed whether the observed spatial patterns (i.e., the hierarchy among landscape units) remain consistent across seasons, determining whether the unit with the highest and lowest diversity varies seasonally or remains constant.

## MATERIALS AND METHODS

### Study area

The Arroyo Saladillo basin is located between latitudes 32°55'S and 33°30'S and longitudes 60°35'W and 61°55'W (southern Santa Fe Province, Argentina), covering parts of the Rosario, San Lorenzo, Caseros, Constitución, and General López departments (Fig. 1). It spans approximately 3144 km², with elevation ranging from 115.5 m.a.s.l. to 18.5 m.a.s.l. The main channel flows in a W–SW to E–NE direction, draining into the Paraná River. The hydrographic network includes several permanent natural and artificial channels. The main watercourse is the Arroyo Saladillo, into which secondary channels such as Arroyo Candelaria, Sanford–Arequito Canal, Arroyo Pueblo Álvarez, Arroyo La Adela–La Esperanza, and Bombal Canal converge, among others. Mean annual precipitation is 1000 mm, distributed throughout the year with higher values between October and April. The middle basin is located between 33°30' and 33° S latitude and 61°30' and 61° W longitude.

In most of the upper and middle basin, soils are well drained, with moderate to moderately slow permeability, not prone to waterlogging and suitable for agriculture. In other sectors of the upper basin and in floodplains of watercourses, soils show imperfect drainage, leading to waterlogging problems (Mendez Zacarías & Zimmermann 2011).

### Landscape units

In general terms, we distinguished three landscape components in the study area: the matrix, characterized by continuity, regularity, homogeneity, and, primarily, dominating the landscape due to its larger area relative to other components; patches, which are irregular polygonal or circular areas representing smaller, discrete habitat units within the matrix; and corridors, which are characterized by their key role in facilitating connectivity among all landscape units and by their elongated shape, in which one dimension (length) predominates over the other (width).

Based on this definition, we established four landscape units:

1) Highly simplified matrix (M1): characterized by annual double-cropping wheat/soybean, which has replaced former crop–livestock rotation systems. Transgenic glyphosate-resistant soybean predominates, favoring the adoption of no-till agriculture over more traditional practices.

2) Low-simplification matrix (M2): includes farms where multiple production systems coexist, generally agricultural–livestock systems, which may or may not incorporate agroecological practices. These areas show greater vegetation heterogeneity due to the presence of sown or natural pastures and sections with exotic or native trees maintained for shade and livestock functional purposes.

3) Patches (P): mainly composed of introduced tree species associated with former rural homesteads, such as *Eucalyptus* sp., *Melia azedarach*, and *Ligustrum* sp., although native species persist at low frequency, including Ceibo (*Erythrina crista-galli*), Ombú (*Phytolacca dioica*), Tala (*Celtis tala*), and White Algarrobo (*Prosopis alba*).

4) Corridor (C): defined by the Arroyo Saladillo channel as its main axis. Its extent depends on multiple environmental factors, particularly topography, which often limits agricultural activity (irregular relief such as undulations, depressions, and hills). As a result, it allows the persistence of natural or semi-natural habitats such as forests, shrublands, and grasslands.

### Sampling

We established three sampling sites for each of the four landscape units (12 sites in total; Fig. 1). Sites were selected to represent all landscape units and to adequately cover the spatial extent of the middle basin of the Arroyo Saladillo. At each site, we established three 500 m transects separated by 100 m. Along each transect, we placed five fixed-radius count points (50 m), each lasting 15 min and separated by 100 m (Ralph et al. 1996). We recorded all birds detected within the radius, regardless of height. Birds in flight actively using the space (hunting, foraging, or moving between trees) were included.

Counts were conducted at each point twice per season over two consecutive years (2021–2022): once in the morning (starting 20 min after sunrise and up to 4 h after) and once in the afternoon (near sunset), following Villarreal et al. (2004). Counts were performed by two observers using binoculars.

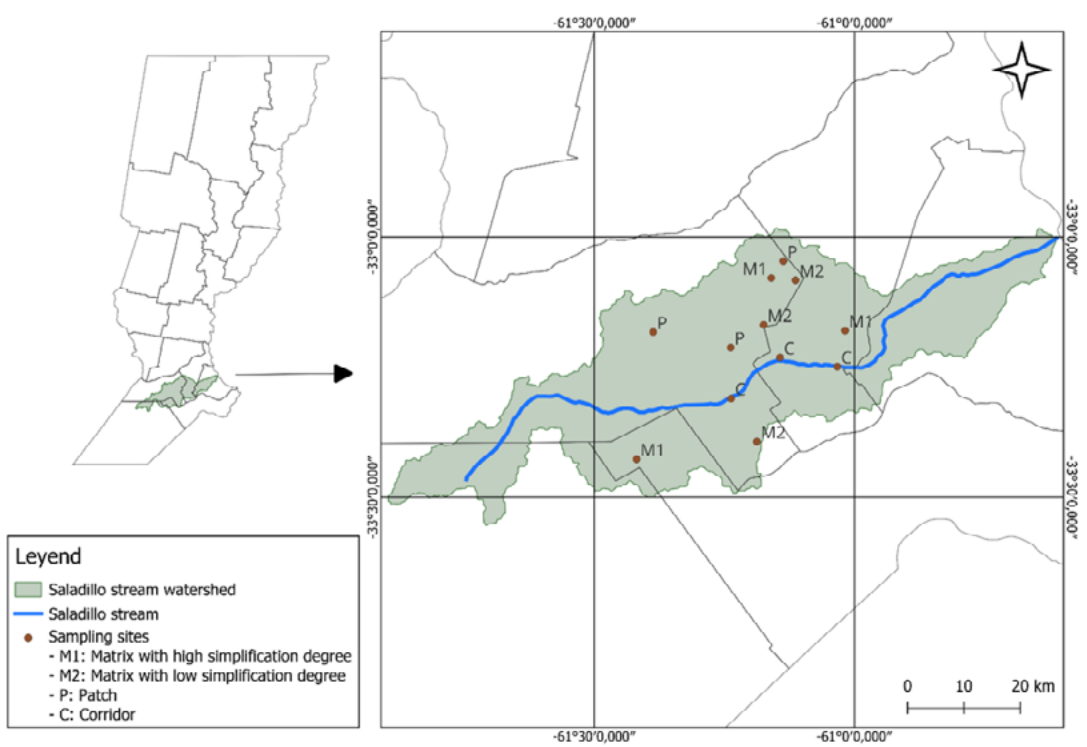


**Figure 1.** Delineation of the study area in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Each point represents a sampling site. Legend: C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

### Trophic guilds

We classified species into trophic guilds based on dietary information from *Birds of the World* (Billerman et al. 2025). Following Foncea et al. (2023), guilds were grouped into six categories according to the main dietary item: omnivores, granivores, nectarivores, herbivores, carnivores, and insectivores. The herbivore category includes both frugivores and folivores.

### Statistical analyses

To characterize assemblages, we quantified total abundance (number of individuals recorded), species richness (number of species), and diversity using the Shannon–Wiener index (H'). This index simultaneously integrates richness and evenness (Moreno 2001, Magurran & McGill 2011) and was expressed as true diversity or effective number of species through the transformation D = exp(H') (Jost 2006).

We generated rarefaction curves (observed richness, S obs.) and non-parametric richness estimators (Chao 2, Jack 2, Bootstrap, and ICE) for each landscape unit, presented in five independent figures, each including the four corresponding curves per landscape unit (Magurran 1988, Colwell & Coddington 1994, Moreno 2001). Rarefaction curves were used to evaluate sampling effort and its adequacy for comparisons among landscape units.

To compare assemblage composition among landscape units, we used the Jaccard index together with cluster analysis, non-metric multidimensional scaling (NMDS), and PERMANOVA. The Jaccard index was calculated from a presence–absence matrix constructed for each landscape unit using the 'vegdist' function in the *vegan* 2.7-2 package in R version 4.5.2 (R Core Team 2025), specifying the 'jaccard' method and binary standardization. The resulting values were used to estimate pairwise similarity among landscape units and to perform hierarchical clustering using the UPGMA method (Unweighted Pair Group Method with Arithmetic Mean).

We implemented NMDS on a Bray–Curtis dissimilarity matrix derived from species abundance data. We used two dimensions and 999 permutations to assess solution stability, and we evaluated model fit using stress values. In addition, we applied PERMANOVA (with 999 permutations) on the same dissimilarity matrix, estimating the proportion of variance explained by landscape unit type ($R^2$) and its significance ($p$). These analyses were performed in R version 4.5.2 (R Core Team 2025). Ordination and community comparison analyses were conducted using the *vegan* 2.7-2 and *permute* 0.9-8 packages. Visualizations were produced with *ggplot2* 4.0.1 and data manipulation with *dplyr* 1.1.4.

To account for spatial dependence among observations from the same site, we complemented analyses with generalized linear mixed models (GLMMs) using the 'glmmTMB' function in R (R Core Team 2025). Site was included as a random factor (1 | site) to account for non-independence within spatial units. Fixed factors were landscape unit (C, P, M1, M2), season (winter, autumn, spring, summer), and year (2021, 2022), as well as two-way interactions 'landscape unit' with 'season', and 'lanscape unit' with 'year'.

For abundance, Poisson and negative binomial models showed convergence and fit issues, so we modeled the log-transformed variable (log(abundance + 1)) using a Gaussian distribution (family = gaussian), which satisfied model assumptions. For richness, we used a Poisson distribution (family = poisson), and for the Shannon index (H'), a Gaussian distribution.

Significance of fixed terms and interactions was assessed using the 'drop1()' function with chi-square tests. When interactions were significant, post hoc comparisons among landscape units within each season were performed using the *emmeans* package with Tukey adjustment.

Model adequacy was evaluated through residual simulations using the *DHARMa* package, with no relevant deviations from assumptions detected in any model.

We assessed trophic guild associations with landscape units using an indicator species analysis with the 'multipatt' function from the *indicspecies* package (v1.7.14). We used the IndVal.g statistic on a presence–absence matrix of guilds per landscape unit, with 999 permutations to assess significance ($\alpha = 0.05$).

## RESULTS

We recorded a total of 25,302 birds (hereafter, records) belonging to 110 species, 39 families, and 17 orders. The best-represented order was Passeriformes, with 18 families and 62 species, accounting for 56.3% of the avifauna recorded in this study (Table 1).

Regarding trophic guilds, 52% of species belonged to the group of birds that feed primarily on invertebrates, followed by omnivores (14%), carnivores (11%), herbivores and granivores (9% each), and frugivores and nectarivores (2% each).

**Table 1.** Bird species recorded in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina, according to presence records at each sampling site. X indicates presence and 0 indicates absence.

| Scientific name | Common name | Location | | | |
|---|---|---|---|---|---|
| | | C | P | M1 | M2 |
| Family: Tinamidae | | | | | |
| *Nothura maculosa* | Spotted Nothura | X | X | X | X |
| Family: Anatidae | | | | | |
| *Cygnus melancoryphus* | Black-necked Swan | X | 0 | 0 | 0 |
| *Callonetta leucophrys* | Ringed Teal | X | 0 | 0 | 0 |
| *Amazonetta brasiliensis* | Brazilian Teal | X | 0 | X | 0 |
| *Spatula versicolor* | Silver Teal | X | 0 | 0 | 0 |
| *Anas georgica* | Yellow-billed Pintail | X | 0 | 0 | 0 |
| *Anas flavirostris* | Yellow-billed Teal | X | 0 | 0 | 0 |
| Family: Columbidae | | | | | |
| *Columba livia* | Rock Pigeon | X | X | X | X |
| *Patagioenas picazuro* | Picazuro Pigeon | X | X | X | X |
| *Patagioenas maculosa* | Spot-winged Pigeon | X | X | X | 0 |
| *Zenaida auriculata* | Eared Dove | X | X | X | X |
| *Columbina picui* | Picui Ground Dove | X | X | X | X |
| Family: Cuculidae | | | | | |
| *Guira guira* | Guira Cuckoo | X | X | X | X |
| Family: Ciconiidae | | | | | |
| *Mycteria americana* | Wood Stork | X | 0 | 0 | 0 |
| *Ciconia maguari* | Maguari Stork | X | 0 | 0 | 0 |
| Family: Rallidae | | | | | |
| *Fulica rufifrons* | Red-fronted Coot | X | 0 | 0 | 0 |
| Family: Threskiornithidae | | | | | |
| *Plegadis chihi* | White-faced Ibis | X | 0 | 0 | 0 |
| Family: Ardeidae | | | | | |
| *Nycticorax nycticorax* | Black-crowned Night Heron | X | 0 | 0 | 0 |
| *Ardea cocoi* | Cocoi Heron | X | 0 | 0 | 0 |
| *Syrigma sibilatrix* | Whistling Heron | X | X | X | X |
| *Egretta thula* | Snowy Egret | X | X | 0 | 0 |
| *Butorides striata* | Striated Heron | X | 0 | 0 | 0 |
| *Ardea ibis* | Western Cattle-Egret | X | 0 | 0 | 0 |
| Family: Phalacrocoracidae | | | | | |
| *Nannopterum brasilianum* | Neotropic Cormorant | X | 0 | 0 | 0 |

| Scientific name | Common name | Location | | | |
|---|---|---|---|---|---|
| | | C | P | M1 | M2 |
| Family: Recurvirostridae | | | | | |
| *Himantopus mexicanus* | Black-necked Stilt | X | 0 | 0 | 0 |
| Family: Charadriidae | | | | | |
| *Vanellus chilensis* | Southern Lapwing | X | X | X | X |
| Family: Scolopacidae | | | | | |
| *Tringa solitaria* | Solitary Sandpiper | X | 0 | 0 | 0 |
| *Tringa flavipes* | Lesser Yellowlegs | X | 0 | 0 | 0 |
| *Tringa melanoleuca* | Greater Yellowlegs | X | 0 | 0 | 0 |
| Family: Tytonidae | | | | | |
| *Tyto furcata* | American Barn Owl | 0 | X | X | 0 |
| Family: Strigidae | | | | | |
| *Athene cunicularia* | Burrowing Owl | X | X | X | 0 |
| *Megascops choliba* | Tropical Screech-Owl | X | 0 | X | 0 |
| Family: Accipitridae | | | | | |
| *Elanus leucurus* | White-tailed Kite | X | X | X | 0 |
| *Rupornis magnirostris* | Roadside Hawk | X | X | X | X |
| *Parabuteo unicinctus* | Harris's Hawk | 0 | X | 0 | 0 |
| Family: Alcedinidae | | | | | |
| *Chloroceryle amazona* | Amazon Kingfisher | X | 0 | 0 | 0 |
| *Chloroceryle americana* | Green Kingfisher | X | 0 | 0 | 0 |
| Family: Picidae | | | | | |
| *Colaptes melanochloros* | Green-barred Woodpecker | X | X | X | 0 |
| *Melanerpes candidus* | White Woodpecker | 0 | X | 0 | 0 |
| *Colaptes campestris* | Campo Flicker | X | X | X | 0 |
| Family: Falconidae | | | | | |
| *Caracara plancus* | Crested Caracara | X | X | X | 0 |
| *Daptrius chimango* | Chimango Caracara | X | X | X | X |
| *Falco sparverius* | American Kestrel | X | X | X | X |
| *Falco femoralis* | Aplomado Falcon | X | X | X | 0 |
| Family: Psittacidae | | | | | |
| *Myiopsitta monachus* | Monk Parakeet | X | X | X | X |
| Family: Caprimulgidae | | | | | |
| *Systellura longirostris* | Band-winged Nightjar | 0 | X | 0 | 0 |
| Family: Trochilidae | | | | | |
| *Hylocharis chrysura* | Gilded Hummingbird | 0 | X | 0 | 0 |
| *Chlorostilbon lucidus* | Glittering-bellied Emerald | X | X | X | 0 |

| Scientific name | Common name | Location | | | |
|---|---|---|---|---|---|
| | | C | P | M1 | M2 |
| Family: Thamnophilidae | | | | | |
| *Taraba major* | Great Antshrike | X | X | 0 | 0 |
| Family: Furnariidae | | | | | |
| *Lepidocolaptes angustirostris* | Narrow-billed Woodcreeper | 0 | X | 0 | 0 |
| *Furnarius rufus* | Rufous Hornero | X | X | X | X |
| *Cinclodes fuscus* | Buff-winged Cinclodes | X | 0 | 0 | 0 |
| *Phacellodomus sibilatrix* | Little Thornbird | X | X | 0 | 0 |
| *Phacellodomus striaticollis* | Freckle-breasted Thornbird | X | 0 | 0 | 0 |
| *Anumbius annumbi* | Firewood-gatherer | X | 0 | 0 | 0 |
| *Schoeniophylax phryganophilus* | Chotoy Spinetail | X | 0 | X | 0 |
| *Synallaxis albescens* | Pale-breasted Spinetail | 0 | 0 | X | 0 |
| *Synallaxis frontalis* | Sooty-fronted Spinetail | X | X | 0 | 0 |
| Family: Tyrannidae | | | | | |
| *Serpophaga nigricans* | Sooty Tyrannulet | X | X | 0 | 0 |
| *Serpophaga subcristata* | White-crested Tyrannulet | X | X | X | 0 |
| *Serpophaga griseicapilla* | Straneck's Tyrannulet | 0 | 0 | X | 0 |
| *Elaenia parvirostris* | Small-billed Elaenia | 0 | X | 0 | 0 |
| *Pitangus sulphuratus* | Great Kiskadee | X | X | X | X |
| *Machetornis rixosa* | Cattle Tyrant | X | X | X | 0 |
| *Myiodynastes maculatus* | Streaked Flycatcher | X | X | 0 | 0 |
| *Tyrannus melancholicus* | Tropical Kingbird | X | 0 | X | 0 |
| *Tyrannus savana* | Fork-tailed Flycatcher | X | X | X | 0 |
| *Pyrocephalus rubinus* | Vermilion Flycatcher | X | X | 0 | 0 |
| *Lessonia rufa* | Austral Negrito | X | 0 | X | 0 |
| *Hymenops perspicillatus* | Spectacled Tyrant | X | 0 | 0 | 0 |
| *Knipolegus aterrimus* | White-winged Black-Tyrant | 0 | X | X | 0 |
| *Neoxolmis coronatus* | Black-crowned Monjita | X | 0 | X | 0 |
| *Xolmis irupero* | White Monjita | X | 0 | 0 | 0 |
| *Myiophobus fasciatus* | Bran-colored Flycatcher | X | X | 0 | 0 |
| *Myiarchus swainsoni* | Swainson's Flycatcher | X | 0 | 0 | 0 |
| Family: Vireonidae | | | | | |
| *Vireo chivi* | Chivi Vireo | 0 | X | 0 | 0 |
| Family: Hirundinidae | | | | | |
| *Tachycineta leucorrhoa* | White-rumped Swallow | X | 0 | X | X |
| *Progne tapera* | Brown-chested Martin | X | X | X | 0 |
| *Progne chalybea* | Gray-breasted Martin | 0 | 0 | X | 0 |

| Scientific name | Common name | Location | | | |
|---|---|---|---|---|---|
| | | C | P | M1 | M2 |
| *Pygochelidon cyanoleuca* | Blue-and-white Swallow | 0 | X | X | 0 |
| Family: Polioptilidae | | | | | |
| *Polioptila dumicola* | Masked Gnatcatcher | X | X | X | 0 |
| Family: Troglodytidae | | | | | |
| *Troglodytes musculus* | Southern House Wren | X | X | X | X |
| Family: Mimidae | | | | | |
| *Mimus saturninus* | Chalk-browed Mockingbird | X | X | X | X |
| *Mimus triurus* | White-banded Mockingbird | X | X | X | 0 |
| Family: Turdidae | | | | | |
| *Turdus rufiventris* | Rufous-bellied Thrush | X | X | X | 0 |
| *Turdus amaurochalinus* | Creamy-bellied Thrush | X | X | X | 0 |
| Family: Passeridae | | | | | |
| *Passer domesticus* | House Sparrow | X | X | X | X |
| Family: Motacillidae | | | | | |
| *Anthus furcatus* | Short-billed Pipit | X | 0 | 0 | 0 |
| Family: Fringillidae | | | | | |
| *Spinus magellanicus* | Hooded Siskin | X | X | X | 0 |
| Family: Passerellidae | | | | | |
| *Ammodramus humeralis* | Grassland Sparrow | 0 | 0 | X | X |
| *Zonotrichia capensis* | Rufous-collared Sparrow | X | X | X | X |
| Family: Icteridae | | | | | |
| *Leistes superciliaris* | White-browed Meadowlark | X | X | 0 | X |
| *Molothrus rufoaxillaris* | Screaming Cowbird | X | X | X | X |
| *Molothrus bonariensis* | Shiny Cowbird | X | X | X | X |
| *Agelaioides badius* | Grayish Baywing | X | X | X | X |
| *Chrysomus ruficapillus* | Chestnut-capped Blackbird | X | 0 | 0 | 0 |
| Family: Parulidae | | | | | |
| *Geothlypis velata* | Southern Yellowthroat | 0 | X | X | 0 |
| *Setophaga pitiayumi* | Tropical Parula | X | X | X | 0 |
| Family: Cardinalinae | | | | | |
| *Piranga flava* | Hepatic Tanager | 0 | X | 0 | 0 |
| Family: Thraupidae | | | | | |
| *Embernagra platensis* | Great Pampa-Finch | X | 0 | X | 0 |
| *Saltatricula multicolor* | Many-colored Chaco Finch | X | 0 | 0 | 0 |
| *Coryphospingus cucullatus* | Red-crested Finch | 0 | X | 0 | 0 |
| *Rauenia bonariensis* | Blue-and-yellow Tanager | 0 | X | X | 0 |

| Scientific name | Common name | Location | | | |
|---|---|---|---|---|---|
| | | C | P | M1 | M2 |
| *Sporophila caerulescens* | Double-collared Seedeater | X | X | X | 0 |
| *Microspingus melanoleucus* | Black-capped Warbling Finch | X | X | 0 | 0 |
| *Sicalis flaveola* | Saffron Finch | X | X | X | X |
| *Sicalis luteola* | Grassland Yellow-Finch | X | X | X | X |
| *Paroaria coronata* | Red-crested Cardinal | X | X | X | 0 |
| *Paroaria capitata* | Yellow-billed Cardinal | X | 0 | 0 | 0 |
| Family: Sturnidae | | | | | |
| *Sturnus vulgaris* | Common Starling | X | X | X | X |

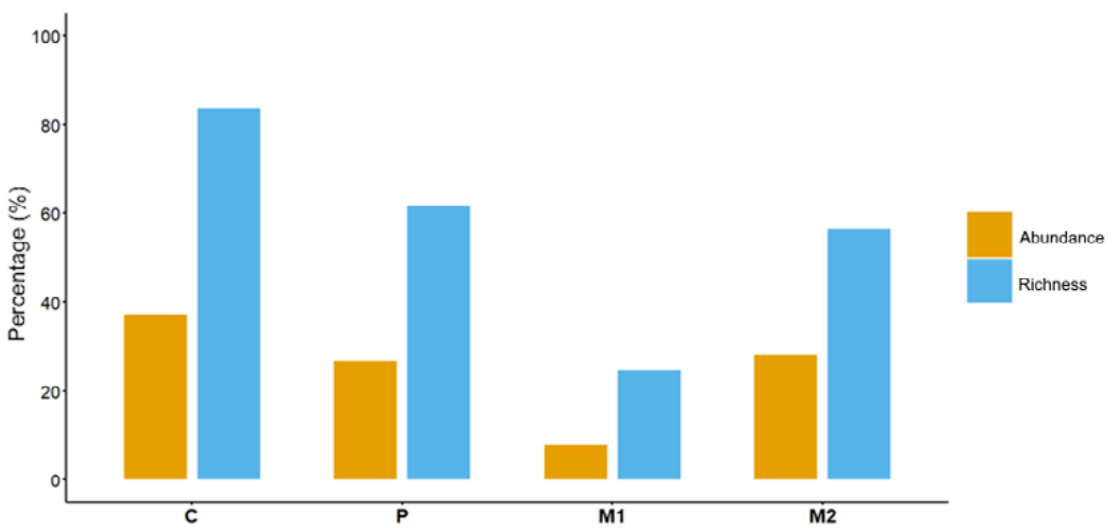


**Figure 2.** Percentage distribution of bird abundance and species richness among the habitats surveyed in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Legend: C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

### Comparison of bird assemblage structure among landscape units

In the corridor, we obtained 9386 records (37% of the total) and a richness of 92 species (83.6% of the recorded species). In the highly simplified matrix (M1), we obtained 1994 records (7.8%) and 27 species (24.5%). In the low-simplification matrix (M2), we obtained 7126 records (28.1%) and 62 species (56.3%). Finally, in the patches, we obtained 6798 records (26.8%) and 68 species (61.8%; Fig. 3).

Based on the behavior of richness estimators for each landscape unit, it seems unlikely that a higher number of species than those recorded would be obtained even with increased sampling effort, as species accumulation curves tended to stabilize (Fig. 4).

To facilitate the ecological interpretation of diversity values, we calculated true diversity (D = exp(H')). The values obtained were the following: C = 55.780, P = 38.910, M1 = 15.880, and M2 = 28.820, indicating that the corridor harbors the highest effective number of species, while M1 maintains the lowest effective diversity.

### Comparison of species composition among landscape units

The Jaccard similarity coefficient showed low similarity in species composition between the highly simplified matrix (M1) and the other landscape units

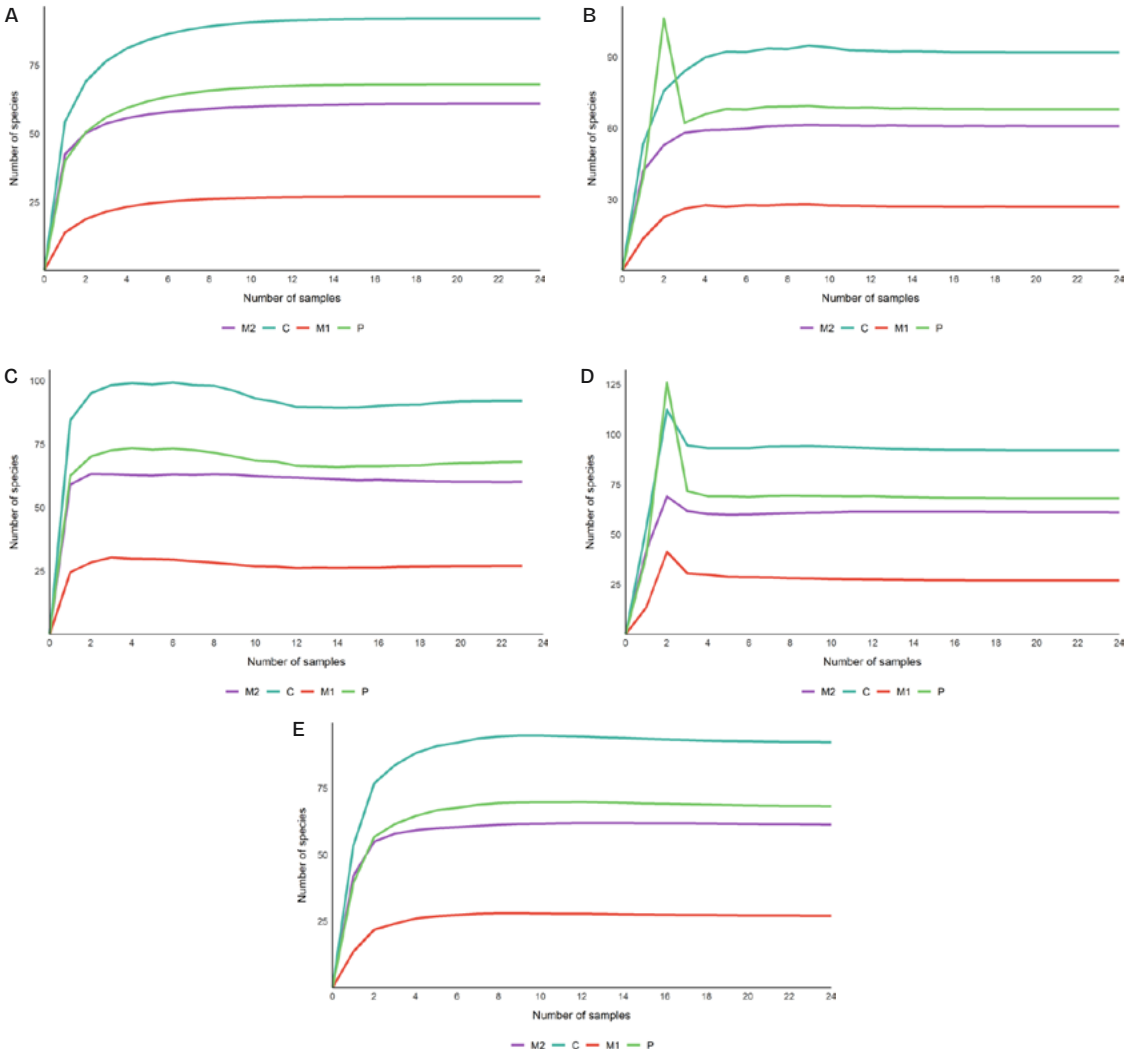


**Figure 3.** Species accumulation curves (S obs) and nonparametric species richness estimator curves for the four landscape units in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. (A) Observed richness (S obs), (B) ICE, (C) Chao 2, (D) Jack 2, and (E) Bootstrap. Each panel shows the curves for the four landscape units: corridor (C), patches (P), highly simplified matrix (M1), and low-simplification matrix (M2).

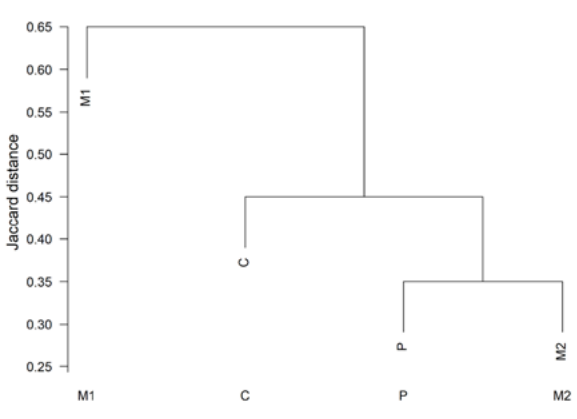


**Figure 4.** Hierarchical clustering dendrogram of bird species composition based on the Jaccard similarity index for each sampling site in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Legend: C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

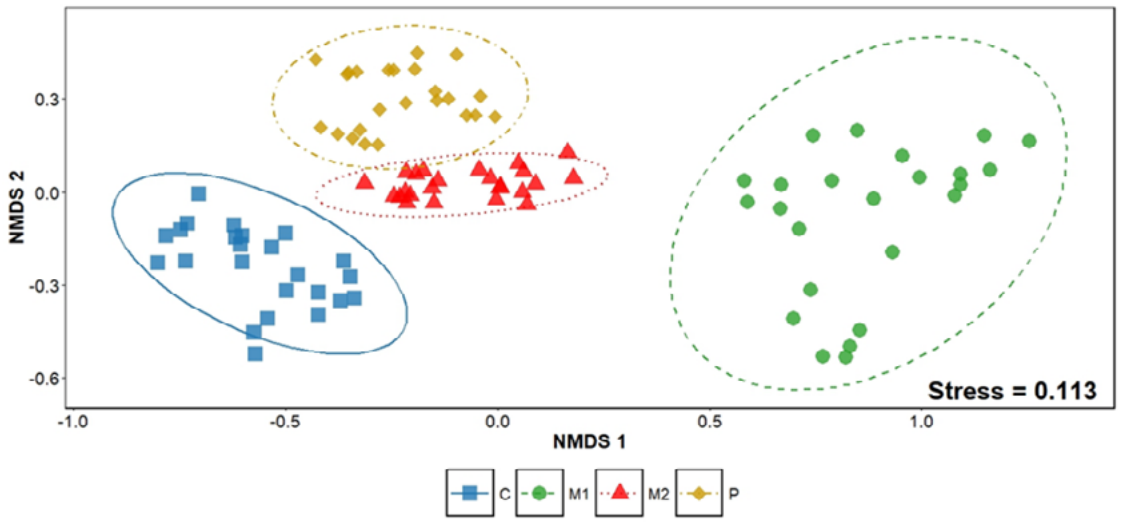


**Figure 5.** Non-metric multidimensional scaling (NMDS) ordination of bird species composition across four habitats in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Legend: C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

(corridor, patches, and low-simplification matrix), with values of J = 0.280, 0.360, and 0.430, respectively. The most similar landscape units were patches (P) and the low-simplification matrix (M2; J = 0.620), which also showed relatively high similarity with the corridor (0.510 and 0.520, respectively; Fig. 5).

These patterns are consistent with the NMDS, which showed a clear segregation among the four landscape units, indicating marked differences in species composition (Fig. 6). Sites clustered consistently in ordination space according to landscape unit, with the corridor showing the greatest differentiation from the highly simplified matrix (M1), while the low-simplification matrix (M2) and patches (P) showed more similar compositions. The PERMANOVA confirmed that landscape unit type explained a significant proportion of the observed variation ($R^2$ = 0.545, $p$ = 0.001), indicating that each landscape unit harbors a distinct bird assemblage (Fig. 6).

### Comparison of trophic guilds among landscape units

The distribution of trophic guilds varied among landscape units. In the corridor (C), patches (P), and the low-simplification matrix (M2), approximately half of the species were insectivorous. In contrast, in the highly simplified matrix (M1), this proportion decreased to 30%, where granivorous species predominated (37%). Omnivores reached their highest proportion in M2 (21%), with no major differences among the other units. Carnivores were most represented in C (12%), followed by P and M2 (9% each),

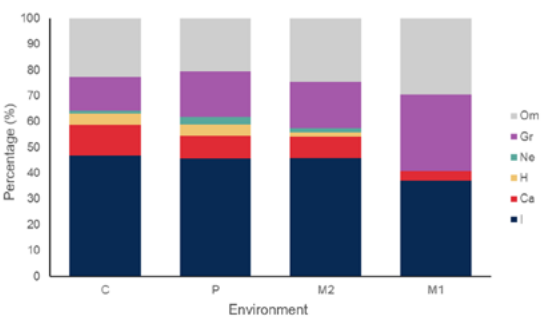


**Figure 6.** Percentage distribution of trophic guilds across the different habitats studied in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Legend: Habitats: C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch). Trophic guilds: Om (Omnivores); Gr (Granivores); Ne (Nectarivores); He (Herbivores); Ca (Carnivores); In (Insectivores).

while no species from this group were recorded in M1.

The indicator species analysis ('multipatt') showed statistically significant associations of carnivorous, herbivorous, and nectarivorous guilds with specific landscape units ($p$ < 0.000 in all cases). These three guilds were mainly associated with C, M2, and P and showed no association with M1. In contrast, omnivorous, granivorous, and insectivorous guilds did not show affinity for any particular unit, occurring broadly across all four landscape units.

### Seasonal variation of bird assemblages among Landscape units

The GLMMs showed a significant interaction between landscape unit and season for all three

analyzed variables (abundance: $\chi^2 = 92.410$, df = 9, $p < 0.001$; richness: $\chi^2 = 17.980$, df = 9, $p = 0.035$; diversity: $\chi^2 = 92.980$, df = 9, $p < 0.001$).

Post hoc Tukey comparisons revealed a consistent pattern across all seasons (Figs. 7, 8, 9): the corridor (C) showed the highest values, the highly simplified matrix (M1) the lowest, while patches (P) and the low-simplification matrix (M2) showed intermediate values with no significant differences between them in most seasons, particularly in spring (abundance and diversity: $p = 0.999$; richness: $p = 0.975$).

This pattern indicates that the hierarchy C > M2 = P > M1 is maintained throughout the year, although the magnitude of differences fluctuates seasonally.

The interaction between landscape unit and year was not significant for any of the variables ($p > 0.050$ in all cases), indicating that the observed patterns remained consistent between 2021 and 2022.

## DISCUSSION

The analyses conducted in the present study highlight and reinforce not only the importance and role of patches and biological corridors in highly anthropized landscapes, but also the potential of diversified production systems to increase connectivity among ecosystem remnants of high conservation value. The results suggest that diversified production systems embedded within the dominant matrix as low-simplification areas (M2) provide a more complex and heterogeneous habitat for wildlife than conventional agricultural fields (M1), as they support greater bird richness and diversity, variables that are positively associated with habitat heterogeneity (Frutos et al. 2016). This structural diversity, at both the vertical and horizontal levels, provides a greater abundance and variety of microhabitats for birds, allowing them to select optimal sites to establish territories and complete their life cycles. In the present study, the low-simplification matrix (M2) tended to function similarly to patches (P) in terms of bird richness, abundance, and diversity, whereas the highly simplified matrix (M1) supported the most depauperate assemblages. Species recorded that may contribute to the control of rodent disease vectors associated with croplands include, for example, *Tyto furcata*, *Rupornis magnirostris*, and *Falco sparverius*. Biondi et al. (2005) described *Daptrius chimango* as a predator of several species of the family Scarabaeidae, which are known to damage a variety of crops. Likewise, some birds of prey play an important role in agroecosystems by contributing to the biological control of species that can

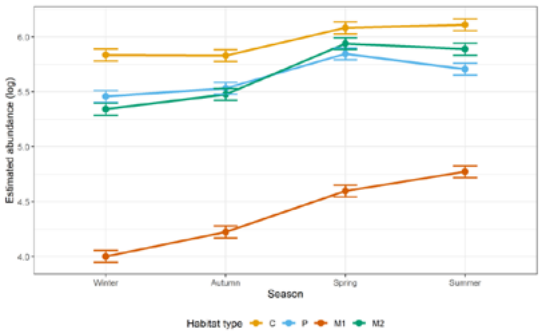


**Figure 7.** Estimated values from the generalized linear mixed model (GLMM) for bird abundance (log scale) across the four landscape units (C, P, M1, M2) throughout the seasons of the year in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Error bars represent 95% confidence intervals. Legend: Sum (summer); Aut (autumn); Win (winter); Spr (spring); C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

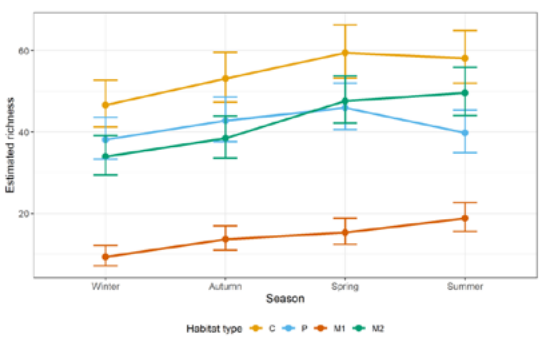


**Figure 8.** Estimated values from the generalized linear mixed model (GLMM) for species richness across the four landscape units (C, P, M1, M2) throughout the seasons of the year in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Error bars represent 95% confidence intervals. Legend: Sum (summer); Aut (autumn); Win (winter); Spr (spring); C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

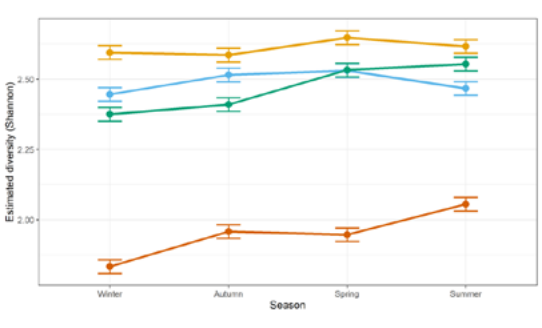


**Figure 9.** Estimated values from the generalized linear mixed model (GLMM) for the Shannon–Wiener diversity index across the four landscape units (C, P, M1, M2) throughout the seasons of the year in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Error bars represent 95% confidence intervals. Legend: Sum (summer); Aut (autumn); Win (winter); Spr (spring); C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

affect crops, such as parakeets and doves (Sergio et al. 2008). However, some of these birds are scavengers and perform equally important ecological functions by removing organic remains, facilitating nutrient recycling, and reducing the proliferation of infectious sources that could promote zoonotic diseases (Morales-Reyes et al. 2015). Together, both groups contribute to the regulation and ecological balance of productive and natural environments.

The largest group of birds recorded belonged to the Passeriformes, which play an important role in controlling invertebrates that may be considered crop pests, as well as in consuming seeds, particularly those of grasses (Alessio et al. 2005, Goijman et al. 2020). Identifying key species that provide ecosystem services may be an appropriate starting point for developing conservation measures (Gorosabel et al. 2020). To achieve this, information that enables long-term population monitoring is essential, since it would allow assessment of how the ecosystem services provided by these species are affected.

The pattern observed for herbivores suggests greater selectivity in habitat use, possibly associated with specific requirements for plant resources available only in certain landscape units. In contrast, the homogeneous distribution of the remaining guilds suggests greater ecological plasticity and a higher capacity to exploit diverse trophic resources across the different habitat types evaluated.

These trends are reflected differently among landscape units, as is clearly evident in the agricultural environment (M1), where granivorous species account for a higher proportion of the assemblage, as reported by Verga et al. (2018) and Codesido et al. (2008). However, unlike Verga et al. (2018), who concluded that habitat fragmentation did not negatively affect the abundance of resources used by birds, our results show a reduction in the number of species in this environment as a consequence of habitat modification. As noted by Codesido et al. (2008), this type of simplification impoverishes the vegetation structure of croplands and their associated habitats, resulting in a decline in resource availability.

The low similarity in species composition between the highly simplified matrix (M1) and the other landscape units (C, P, and M2; J = 0.280, 0.360, and 0.430, respectively) may be associated with the high degree of habitat homogenization in this environment; the intensive use of agrochemicals, which reduces food availability (seeds and insects); and the lower presence of key structural elements such as trees and shrubs that many bird species use for nesting, perching, or foraging. This specialization of the agricultural landscape reduces the assemblage to a few generalist species, resulting in the loss of ecosystem services (Zaccagnini et al. 2011). In this regard, Codesido et al. (2013) reported that total bird abundance, as well as the abundance and richness of grassland specialists, were lower in cropland landscapes than in livestock and mixed-production landscapes. This occurs because crops, particularly under no-till farming and herbicide-tolerant soybean cultivation, simplify habitat structure and reduce roadside vegetation, and agricultural operations may reduce the nesting success of ground-nesting birds. The greater representation of generalist species in bird assemblages of Pampas agroecosystems suggests that agricultural activities that modify habitats often benefit these species, allowing them to become more common (Codesido et al. 2012). The same authors also pointed out that grassland specialist species are among the most vulnerable because of the destruction and fragmentation of their natural habitat by intensive agriculture. Similarly, Zufiaurre et al. (2016) reported that bird assemblages are impoverished in agricultural fields compared with livestock fields, attributing this difference to the greater structural homogeneity of croplands, which simplifies habitat and reduces the number of available niches, whereas livestock fields create greater structural variability and resource diversity through grazing. Annual cropland is therefore more detrimental to bird communities than cattle grazing in Pampas agroecosystems (Codesido et al. 2013). In our study, the highest similarity occurred between patches and the low-simplification matrix (P and M2; J = 0.620), suggesting that fields with lower levels of anthropogenic disturbance that retain natural elements can support part of the biodiversity typically associated with more conserved environments. Azpiroz & Blake (2009), in turn, suggested that planted pastures benefit several common species that do not reach high densities in croplands, but negatively affect birds restricted to native grasslands. Consequently, many Pampas bird species, particularly insectivores and granivores, can use both landscape units, whereas grassland specialists do not use planted pastures, making the conservation of natural remnants essential for their protection.

The patterns observed in the NMDS indicate that species composition differs consistently among landscape units, with clearly segregated communities. The marked separation of the corridor from the other units, together with the relative similarity

between M2 and patches, suggests that the structural characteristics of each environment strongly influence the composition of its bird assemblages. Both approaches (the dendrogram based on the Jaccard coefficient and the NMDS ordination combined with PERMANOVA) evaluated community composition from complementary perspectives: the dendrogram reflects hierarchical similarity relationships, whereas the NMDS describes gradients in multivariate space, reinforcing the observed patterns. These results, supported by the PERMANOVA, reinforce the idea that each environment harbors a distinct bird community, probably associated with differences in vegetation cover, habitat heterogeneity, and resource availability.

In addition, M1 showed the greatest differences relative to the other landscape units in terms of richness, abundance, and diversity. This pattern can be explained by differences in land use, which generate variation in resource availability (Codesido et al. 2008). In particular, seasonal changes in diversity were more pronounced in M1, which is expected considering that the dominant crops in the region are planted in spring and harvested during summer–autumn, leaving fields with little vegetation cover throughout winter. In this regard, Leveau & Leveau (2004) noted that soybean monoculture is based on glyphosate-resistant cultivars and the intensive use of agrochemicals to eliminate weeds, leading to the impoverishment of vegetation structure and a consequent decline in bird abundance. According to Whitford (1997), interannual variation in bird diversity may also be associated with changes in precipitation regimes and with the transformations that vegetation undergoes throughout its phenological cycle.

In contrast, the M2 environment, with a lower degree of anthropogenic disturbance, showed higher values of richness, abundance, and diversity. This environment, characterized by greater ground cover and the presence of extensive livestock production, provides a more heterogeneous vegetation structure that promotes foraging opportunities on invertebrates and seeds (Codesido et al. 2008). Likewise, seasonal changes were less pronounced in this environment, which may be attributed to the effect of permanent pastures and livestock grazing, both of which introduce structural variability into the habitat. The results show that, across the four landscape units studied, bird richness and abundance were highest during spring and summer. These findings are consistent with those of Leveau & Leveau (2011), who attributed this pattern to the arrival of species that are austral migrants. In addition, it may be associated with the search for food and nesting sites, as this period coincides with the breeding season of most bird species.

The greatest seasonal changes were also recorded in M2, with marked declines from summer and spring to autumn. These results differ from those of Leveau et al. (2024), who proposed that greater diversity within landscape units leads to greater stability in bird diversity. Under this hypothesis, M1 would have been expected to exhibit the greatest seasonal variation. However, this discrepancy may be explained by the fact that landscape units such as M2 provide a greater abundance of resources during the breeding season, resulting in increased activity and the presence of species that arrive in search of food and nesting sites. This interpretation is consistent with Zufiaurre et al. (2016), who found that livestock fields consistently supported higher species richness than agricultural fields during spring and summer, whereas landscape units such as M1 consistently maintained low bird abundance and limited species turnover.

Our results indicate that bird diversity in the middle basin of the Arroyo Saladillo varies markedly among seasons, but above all according to land use and land cover in each landscape unit. Environments that retain greater vegetation diversity and experience lower levels of human disturbance, such as biological corridors, patches, and fields managed under more diversified production systems, support a greater abundance and variety of birds throughout the year. These findings highlight the importance of promoting management practices that integrate biodiversity conservation into productive landscapes. They also underscore the need to advance policies that recognize the value of vegetation patches and biological corridors as fundamental components of ecological balance in these highly transformed landscapes.

Regarding seasonal variation, the GLMMs showed that the hierarchy among landscape units remained consistent throughout the year: the corridor (C) exhibited the highest values of abundance, richness, and diversity in every season, whereas the highly simplified matrix (M1) consistently showed the lowest values, with no significant differences between patches (P) and the low-simplification matrix (M2) at any time of the year (post hoc comparisons, $p > 0.05$ in all cases). However, the magnitude of seasonal variation differed among landscape units: the decline in abundance from summer to autumn was more pronounced in C and M2 than in M1 and P (landscape unit × season interaction, $p < 0.001$), whereas the increase in diversity from winter to spring was greater in M2 and M1 than in C ($p = 0.012$). These findings differ

partially from those reported by Zúñiga (2007), who found that spring was the season of highest diversity across all landscape units analyzed, suggesting that seasonal responses may vary according to land cover and land-use type.

Seasonal variation was also reflected in significant differences among most seasons, although summer and spring did not differ from one another. This pattern may be associated with the breeding and parental care period, as well as with seasonal changes in vegetation phenology that increase food availability for birds (Lorenzón et al. 2019, Leveau et al. 2024). Similarly, Codesido & Bilenca (2004) attributed higher bird diversity during these seasons to the greater abundance of invertebrates.

Regarding trophic guilds across the different landscape units, insectivorous birds were the best represented. These findings are consistent with those reported by Salas Correa & Mancera-Rodríguez (2018) and López-Muñoz et al. (2022), highlighting the importance of these trophic resources within the sampled landscape units.

In southern Santa Fe Province, Argentina, where grain and oilseed crops dominate the landscape and have led to a substantial reduction in natural habitats, changes in ecosystem structure and functioning, and, in most cases, habitat fragmentation (Rimoldi 2013), we found that bird assemblages tended to occur more frequently in the more stable landscape units, namely, the Arroyo Saladillo biological corridor, followed by patches and fields with a low degree of simplification. These findings support the proposal of Biasatti & Rimoldi (2022), who suggested implementing reverse fragmentation strategies in the region. This approach involves developing patches and biological corridors within the anthropogenic agroecosystem matrix to interrupt landscape homogeneity and promote biodiversity conservation in landscapes dominated by agricultural production.

### Study limitations

The 100 m spacing between point counts is shorter than the 250 m generally recommended to ensure spatial independence in some sampling designs. This decision was dictated by the characteristics of the patch landscape unit (P), which consists of relatively small habitat areas where greater spacing would have compromised the representativeness of the sampled habitat.

Nevertheless, to account for the potential lack of independence among observations within each site, the analyses were complemented with generalized linear mixed models (GLMMs), including site as a random factor. The results were consistent with the initial analyses, suggesting that the observed patterns are robust despite this methodological limitation.

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# WILD HYBRIDIZATION BETWEEN WHITE-FACED (*Dendrocygna viduata*) AND FULVOUS (*D. bicolor*) WHISTLING DUCKS

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**ABSTRACT:** Wild hybridization between the White-faced Whistling Duck (*Dendrocygna viduata*) and the Fulvous Whistling Duck (*D. bicolor*) has been documented in South Africa, but there are few reports for the Americas. Here, we present seven such records for South America, five in Brazil and two in Argentina. The data show that this biological phenomenon occurs throughout the distribution of these species, but it is rare. The hybrids exhibit a general body pattern like that of the Fulvous Whistling Duck, while details of the head, neck, and wings are more like those of the White-faced Whistling Duck. These records document the occurrence, frequency, and distribution of hybridization among whistling ducks in the Southern Hemisphere, where reports remain scarce.

**KEYWORDS:** *conservation, field observations, South America, urban reservoirs, whistling ducks*

The phenomenon of interspecific hybridization is well known and well documented among birds, and it is believed that nearly 10% of avian species have hybridized in the wild (Grant & Grant 1992). Hybridization in the order Anseriformes, particularly within the family Anatidae (including ducks and whistling ducks), is frequent; approximately 133 species have hybridized, though most hybrids have occurred in captivity, with few records in the wild (Sick 1997, McCarthy 2006).

The genus *Dendrocygna* comprises eight species (AviList Core Team 2025), seven of which have documented cases of hybridization. Of the 23 described cases of hybridization within the genus, only seven involving four species occurred in the wild; the remaining cases occurred in captivity. Within these rare instances of wild hybridization, the White-faced Whistling Duck (*D. viduata*) and the Fulvous Whistling Duck (*D. bicolor*) have been documented to hybridize (Ottenburghs et al. 2015). These species occur together throughout most of their geographic distributions in much of South America and Africa. The Fulvous Whistling Duck also occurs in southern North America, Central America, and parts of Asia (Winkler et al. 2020).

Documented records of wild hybridization between the White-faced Whistling Duck and the Fulvous Whistling Duck are scarce; they include two from South Africa and one from Brazil. The first South African record is from 1972 near Johannesburg (Clark 1974) and the second, involving two detections, from 2012 in the Western Cape (Harebottle & Vanderwalt 2014). Despite both species having overlapping distributions in Brazil, there is only one published record of two cases of wild hybridization recorded in 1989 in the south of the country (Santa Vitória do Palmar, state of Rio Grande do Sul; 33°00'S, 52°50'W, 11 m), involving birds captured during a banding program (Nascimento et al. 1990).

In this article, we provide documented evidence of two records of wild hybridization between

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the White-faced Whistling Duck and the Fulvous Whistling Duck in the city of São Paulo, state of São Paulo, Brazil. We also synthesize and evaluate images of hybrids available on the online bird observation and photography platforms WikiAves – Brazil (https://www.wikiaves.com.br/) and eBird/Macaulay – USA https://www.macaulaylibrary.org/).

The first record was made by WCAB at the lake inside the Parque Zoológico de São Paulo (23°39'S, 46°37'W, 780 m) during working hours. On 25 August 1969, CAB observed a hybrid individual and photographed it along a group of free-living White-faced Whistling Ducks (Fig. 1). Twenty-six days later, on 20 September 1969, the same individual was collected, although the whereabouts of this specimen are unknown (Fig. 1). The individual presented a uniform brown body coloration, similar to that of the Fulvous Whistling Duck, but with a white cheek, reddish-brown chest, streaked flanks, and black beak, nape, and posterior part of the neck, typical of the White-faced Whistling Duck (Fig. 1). We ruled out the possibility of it being a bird bred in captivity, since in that case the images would have been taken either with the bird in hand or with some kind of annotation, as in other cases documented by the same researcher. In the present case, the author annotated the image frame with 'White-faced Whistling Duck x Fulvous Whistling Duck' and 'hybrid'. The images were taken with an analog camera on 35 mm positive film (slides showing age-related damage) and show how WCAB was already using photography as a research tool in


**Figure 1.** Hybrid individual photographed in the wild and subsequently collected at the Parque Zoológico de São Paulo, city of São Paulo, Brazil, in August and September 1969, respectively. A) The hybrid individual is the second from the left in the group of White-faced Whistling Ducks (*Dendrocygna viduata*). B) Lateral and ventral views. C) Legs and flanks. D) Legs and uropygium. E) Upper part of the head, nape, and posterior part of the neck. F) Lower part of the head. Photographs: Bokermann WCA.

the 1960s. The original images are deposited in the library of the Museu de Zoologia da Universidade de São Paulo.

The second record was made in 2022 by FS at the Guarapiranga reservoir, in the southern region of the city of São Paulo (23°45'S, 46°43'W, 735 m), during monthly onboard monitoring of aquatic and migratory birds carried out voluntarily since May 2016. On 26 November 2022, during count number 100 (at approximately 10 AM), a hybrid individual was observed and photographed near a group of approximately 21 White-faced and 100 Fulvous Whistling Ducks in an isolated rural area of the Guarapiranga reservoir called 'Braço do Ribeirão Caulim'. The individual was resting out of the water but became alert with the approach of the boat, flying away immediately afterwards and demonstrating the wary behavior typical of a free-ranging wild bird (Fig. 2). The individual had a uniform brown coloration on its body and head, with wing and side body patterns more similar to the Fulvous Whistling Duck, but with a white cheek and side of the neck; a black beak, nape, back of the neck, and wing feathers; and reddish-brown wing coverts, similar to the White-faced Whistling Duck (Fig. 2). The individual did not vocalize during flight and landed about 300 m away together with another group of White-faced and Fulvous Whistling Ducks.

Consulting the hybrid species pages (for records of hybrids between White-faced Whistling Duck and Fulvous Whistling Duck) of the two main online


**Figure 2.** Hybrid individual documented in the Guarapiranga reservoir, south of the city of São Paulo, Brazil, November 2022. A) Group of White-faced Whistling Ducks (*Dendrocygna viduata*) and Fulvous Whistling Ducks (*D. bicolor*) near the hybrid individual. B & C) Hybrid individual out of the water. D & E) Hybrid individual in flight. Photographs: Schunck F.

**Table 1.** Records of hybrids between the White-faced Whistling Duck (*Dendrocygna viduata*) and the Fulvous Whistling Duck (*D. bicolor*) available on the birdwatching platforms eBird/Macaulay Library (ML) and WikiAves Brasil (WA). The abbreviations ML and WA refer to records with documentation on their respective platforms, while the abbreviation S refers to a list with one undocumented record.

| Image number | Locality | Date | Author |
|---|---|---|---|
| ML210219891 | Reserva Ecológica Costanera Sur, Ciudad Autónoma de Buenos Aires, Argentina | 18 February 2020 | Diego Bastías |
| ML641694873 | Laguna Gualeguay, Entre Ríos, Argentina | 09 January 2025 | Lucas Villafañe |
| WA212951 | Curitiba, Paraná, Brazil | 28 September 2010 | Marcelo Bonat |
| WA2462642 | Mostardas, Rio Grande do Sul, Brazil | 20 December 2016 | Geraldo Apratto Gonçalves |
| S157592008 | São Pedro, São Paulo, Brazil | 31 December 2023 | Paulo Guimaraes |

birdwatching platforms, eBird/Macaulay Library (https://search.macaulaylibrary.org/catalog?taxonCode=x00938&mediaType=photo&sort=rating_rank_desc; 56 records) and WikiAves Brasil (https://www.wikiaves.com.br/midias.php?tm=f&t=s&s=90001; 2 records), up to 8 October 2025, revealed five records of hybrids that we consider to be wild, as they were not classified by the authors as captive birds and were seemingly in natural environments (Table 1). Among these five records, four have photographic documentation, and one contains only descriptive data. Two records were made in Argentina, southern South America (2020 and 2025), and three in Brazil, in the South (Paraná and Rio Grande do Sul) and Southeast (São Paulo) regions in 2010, 2016, and 2023, respectively. The photographed birds present morphological characteristics similar to those herein reported in the city of São Paulo, having the general brown pattern of the Fulvous Whistling Duck, but with the white frontal part of the head and neck closer to the White-faced Whistling Duck (Table 1).

Available records of hybrids between White-faced and Fulvous Whistling Ducks are very scarce in comparison to the sheer number of records available for these two species, but they suffice to show that this phenomenon occurs in both South America and Africa. For example, the Guarapiranga reservoir record occurred during just one out of 131 field trips, providing further evidence of the rarity of hybridization between these two species.

The pooled records reveal a general pattern (mainly in body coloration) most similar to the Fulvous Whistling Duck, with more subtle characteristics of the White-faced Whistling Duck, such as white coloration on the head and neck, reddish-brown on parts of the body, striations on the flanks, and black on the nape and back of the neck. However, each individual displays a unique pattern. The hybrids described for South Africa by Clark (1974) and Harebottle & Vanderwalt (2014) are also similar to those found in the city of São Paulo and online platforms.

There are many flooded areas in the city of São Paulo, and the natural occurrence of ducks of the genus *Dendrocygna*, especially the Fulvous and White-faced Whistling Ducks, has been documented since 1916; they are common and numerous birds in the region (Pinto 1938, Bokermann 1985, São Paulo 2024).

The dissemination of field data obtained in the city of São Paulo and the compilation made using online bird observation platforms are in line with the recommendation made by Harebottle & Vanderwalt (2014) to report cases of hybrids in wild populations of Anatidae. These records are vital for better documenting the occurrence, frequency, and distribution of these hybridizations in the Southern Hemisphere, where reports remain scarce, especially among whistling ducks.

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# DISCOVERY OF TWO NEW COLONIES OF OLROG'S GULL (*Larus atlanticus*) IN THE BAHÍA BLANCA ESTUARY, BUENOS AIRES PROVINCE, ARGENTINA

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**ABSTRACT:** Olrog's Gull (*Larus atlanticus*) is a larid species endemic to the South Atlantic coast and is considered Vulnerable in Argentina. Its breeding range is restricted to estuarine islands characterized by low elevation above sea level, sparse vegetation, and proximity to crab beds. Nearly the entire breeding population nests in protected areas with varying categories of conservation in Buenos Aires Province. During aerial censuses, conducted on 17 October 2025 to update population estimates, we recorded two new breeding sites of Olrog's Gull in the Bahía Blanca estuary: one at the northeastern tip of Trinidad Island (39°05'S, 61°55'W) and the other at the northeastern tip of Ariadna Island (39°14'S, 61°58'W). Both sites are located within the Bahía Blanca, Bahía Falsa, Bahía Verde Nature Reserve. Apparently Occupied Nests, which provide an estimate of the number of breeding pairs, were counted yielding a total of 26 ± 2 ($n$ = 7 photographs) and 22 ± 1 ($n$ = 4 photographs), respectively. The colonies are located close to the tidal line and may therefore be vulnerable to substantial habitat alterations caused by severe storms or human activities such as dredging and recreational use. These sectors are currently outside the reserve's strictly protected zone. As a result of this finding, they have been incorporated into the ongoing revision of the reserve's zoning scheme to strengthen effective protection measures during this critical period for the species.

**KEYWORDS:** *aerial census, colony, Bahía Blanca estuary, Olrog's Gull, Larus atlanticus, population size*

Olrog's Gull (*Larus atlanticus*) is a larid species endemic to the Atlantic coast of South America and can be found during the non-breeding season from southern Argentina to southern Brazil (Yorio et al. 2013). Its breeding range is restricted to estuarine islands, generally shared with the Kelp Gull (*Larus dominicanus*), where it selects sites close to the high-tide line, at relatively low elevations above sea level, with sparse vegetation and in proximity to crab beds (Borboroglu & Yorio 2007). The most recently published population estimates reported only approximately 8,000 breeding pairs (Yorio et al. 2013). This is one of the factors leading to its classification as Vulnerable in Argentina, Endangered in Uruguay (Azpiroz & Caballero-Sadi 2017), and Near Threatened globally (BirdLife International 2025).

The breeding sites reported for the species are located within Buenos Aires Province, Argentina, in the Bahía Blanca estuary (which contains most of the breeding population) and the Bahía San Blas estuary, and marginally in Chubut Province, Argentina (supporting less than 2% of the breeding population; Yorio et al. 2013). The first comprehensive breeding record of the species was reported in Bahía Anegada, within the San Blas area, where approximately 400

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individuals were counted (Devillers 1977). Over the years, 24 sites have been reported as having supported breeding activity at some point (Yorio et al. 2013). Breeding activity is not simultaneously present at all sites; rather, the number of active breeding sites varies annually between six and nine (Yorio et al. 2013). Some colonies have shown continuous activity throughout the monitored years, such as Isla del Puerto, Isla Gaviota, and Islote Arroyo Jabalí Oeste (Yorio et al. 2013). However, other breeding sites are less stable and may change from year to year, allowing for the establishment of new colonies (Yorio et al. 2005, 2013, Petracci et al. 2008), increasing the relevance of the extent of environmental protection measures for potential breeding areas.

Within the Bahía Blanca estuary lies the Bahía Blanca, Bahía Falsa, Bahía Verde Multiple-Use Provincial Nature Reserve (Provincial Law No. 12 101/98), which includes several islands, sandbanks, and surrounding waters, as well as the Islote de la Gaviota Cangrejera Nature Reserve for Fauna and Education (Provincial Law No. 15 362/22). Further south lies the Bahía San Blas Multiple-Use Natural Reserve and Wildlife Refuge (Provincial Law No. 12 788/01). These key areas for biodiversity protection are not only important because they encompass breeding grounds for the species, but also because they protect habitats containing crab beds supporting its principal prey, the Burrowing Crab (*Neohelice granulata*; Delhey et al. 2001a, Herrera et al. 2005, Suárez et al. 2011, Yorio et al. 2013).

To estimate the number of breeding pairs of Olrog's Gull, an aerial census was conducted during the 2025 breeding season in the Bahía Blanca estuary and Bahía San Blas areas.

## METHODS

To conduct the census of the Olrog's Gull colonies, we used a Cessna 182 aircraft flying at an altitude of approximately 100 m to survey the Bahía Blanca estuary on 17 October 2025. The flight route was designed to cover areas with previously reported breeding activity as well as sites exhibiting suitable characteristics for breeding. We took photographs of sites where colonies were observed during the flyover.

Photographs were taken using a Sony Alpha 9 II camera equipped with a Sony 24–240 mm zoom lens, capturing each colony from multiple angles. We selected the photographs that were closest to the colony and of the highest quality. From this subset, we performed manual counts using the image-editing software Inkscape v1.3.2. Values are reported as mean ± standard error and 95% confidence intervals.

We counted Apparently Occupied Nests (Gregory et al. 2004), hereafter referred to as 'nests' for ease of reading, as an estimate of the number of breeding pairs. In this species, nests may be constructed of plant material or be located directly on sand and gravel, often at high densities (Yorio et al. 2001, 2013, Petracci et al. 2008; Fig. 1). Abandoned nests can be recognized by a central depression (Petracci et al. 2008). Accordingly, a nest was identified as a nesting site if it exhibited the characteristics described above and if it had at least one adult nearby. Adults were only associated with a nest when they displayed an unequivocal incubation posture (i.e., positioned over a depression in the substrate; Figs. 1A & 1B). Nests lacking evidence of occupancy (Fig. 1C) or adults resting without such a posture (Fig. 1D) were assumed to belong to another breeding pair and were not counted as nests.

## RESULTS

During the flight conducted over the Bahía Blanca estuary on 17 October 2025, we recorded two new breeding sites of Olrog's Gull: one at the northeastern tip of Trinidad Island, which we named 'Guardaparque Dana Piedrabuena Bank' (39°05'S, 61°55'W), and another at the northeastern tip of Ariadna Island, in an area known as 'Manchín Bank' (39°14'S, 61°58'W; Fig. 2). For the colony near Trinidad Island, we counted a total of 26 ± 2 (24–27) nests ($n$ = 7 photographs). For the colony near Ariadna Island, we counted 22 ± 1 (19–25) nests ($n$ = 4 photographs). No chicks were observed in the photographs. Regarding the breeding stage at the time of sampling, we observed an average of approximately two eggs per nest in a total of 22 nests in the Islote del Puerto/Olrog's Gull Islet area on 30 September 2025.

## DISCUSSION

These results highlight the importance of continuing to monitor the breeding distribution of Olrog's Gull. Breeding stage has been reported to vary among colonies: Suárez et al. (2011) reported incubation occurring between late September and early October in the San Blas area, a period similar to that reported by La Sala et al. (2011) for the Bahía Blanca area. In contrast, Herrera et al. (2005) reported incubation during November in colonies in Chubut Province. Devillers (1977) suggested that breeding asynchrony may also occur within the same area as a consequence

of egg harvesting by local inhabitants. Although this practice is currently believed to persist only illegally at one colony in Bahía San Blas, additional studies are needed to assess its occurrence throughout the breeding range of Olrog's Gull.

The newly identified colonies are located close to the waterline (Fig. 3), with the Ariadna Island colony being particularly exposed and lacking vegetation cover. Consequently, it may be vulnerable to major alterations of emergent estuarine habitats resulting from severe storms (Delhey et al. 2001b, Borboroglu & Yorio 2007, Yorio et al. 2013, Dias et al. 2019, Fiori & Pratolongo 2021). Another reported threat to breeding habitats is the presence of exotic species, such as Barilla plant (*Soda inermis*), which forms dense cover potentially restricting the availability of nesting sites for Olrog's Gull (Marbán & Zalba 2019).

The discovery of these new breeding areas comes at a time when the management plan of the Bahía Blanca, Bahía Falsa, Bahía Verde Nature Reserve is being revised. Their inclusion in the new zoning scheme would place them within the reserve's strictly protected area, together with the other known colonies, thereby strengthening effective protection measures for key breeding habitats during this critical period for the species.

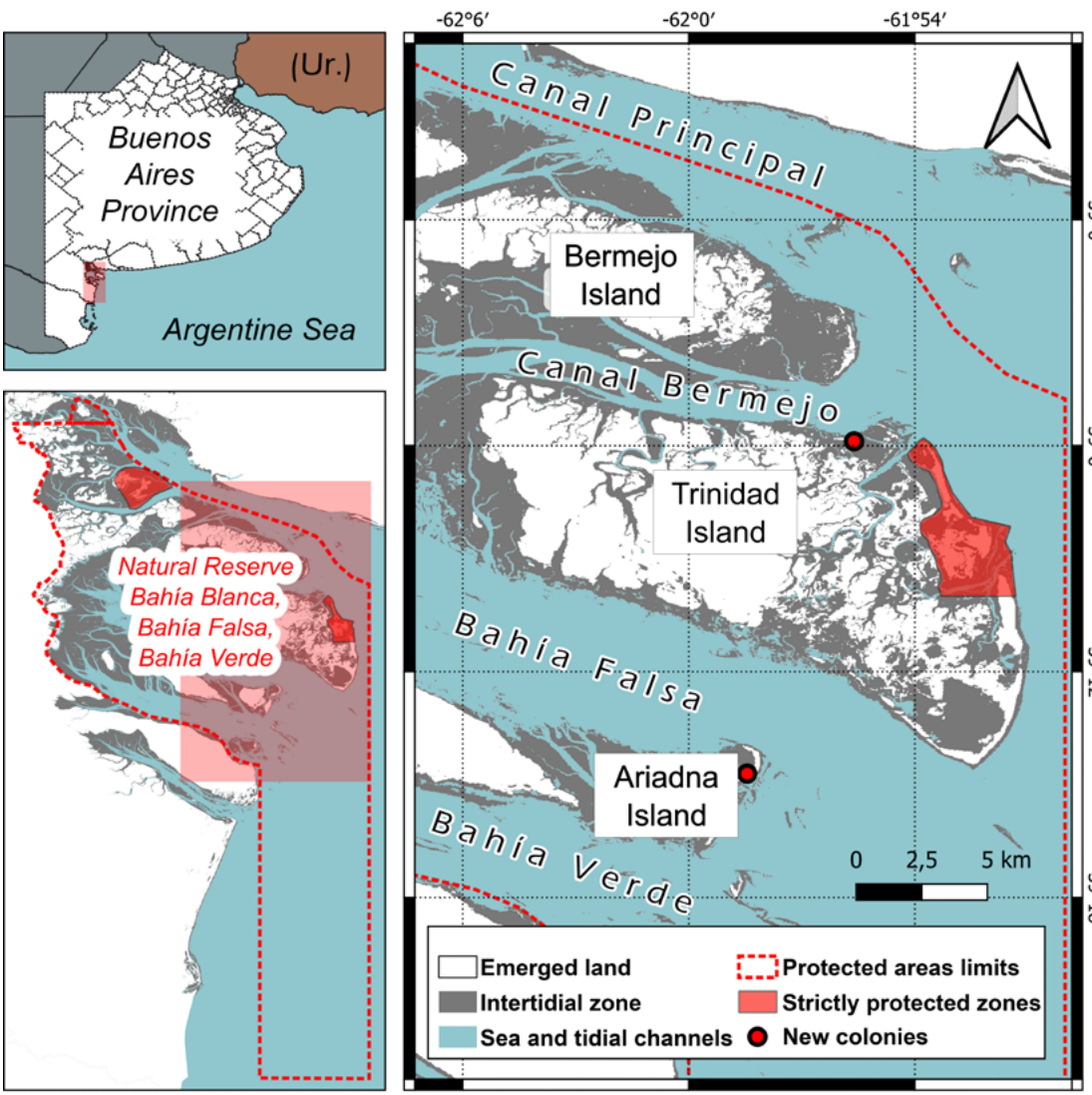


**Figure 1.** Geographic location of the new Olrog's Gull (*Larus atlanticus*) colonies (red points) recorded in 2025 on Ariadna Island and Trinidad Island, Buenos Aires, Argentina. The red dashed line indicates the reserve boundary, and the red shaded rectangles indicate the area shown in detail in the image on the right (map created using QGIS v3.44.7).

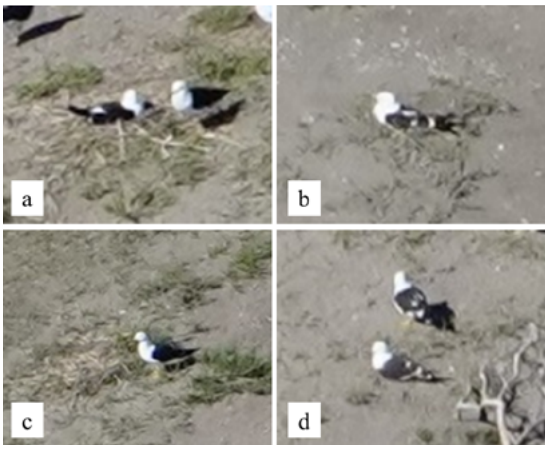


**Figure 2.** Detail of photographs of nests and adults of Olrog's Gull (*Larus atlanticus*) recorded in the Bahía Blanca estuary (Buenos Aires, Argentina), illustrating the criteria used to identify Apparently Occupied Nests. The upper photographs show examples of active nests. A) A typical active nest with one adult sitting (left) and another standing nearby (right). B) An active nest with an adult in an incubation posture over a central depression, without a conspicuous vegetation rim. C) Inactive nests (not counted): a conspicuous vegetation rim is present, but there is no evidence of activity. D) One sitting adult (bottom) and one standing adult (top), not considered an Apparently Occupied Nest.

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In recognition of her outstanding and long-standing dedication, the islet of Trinidad Island where the new colony was recorded was named 'Guardaparque Dana Piedrabuena' in honor of her legacy in biodiversity conservation. The park ranger service will always

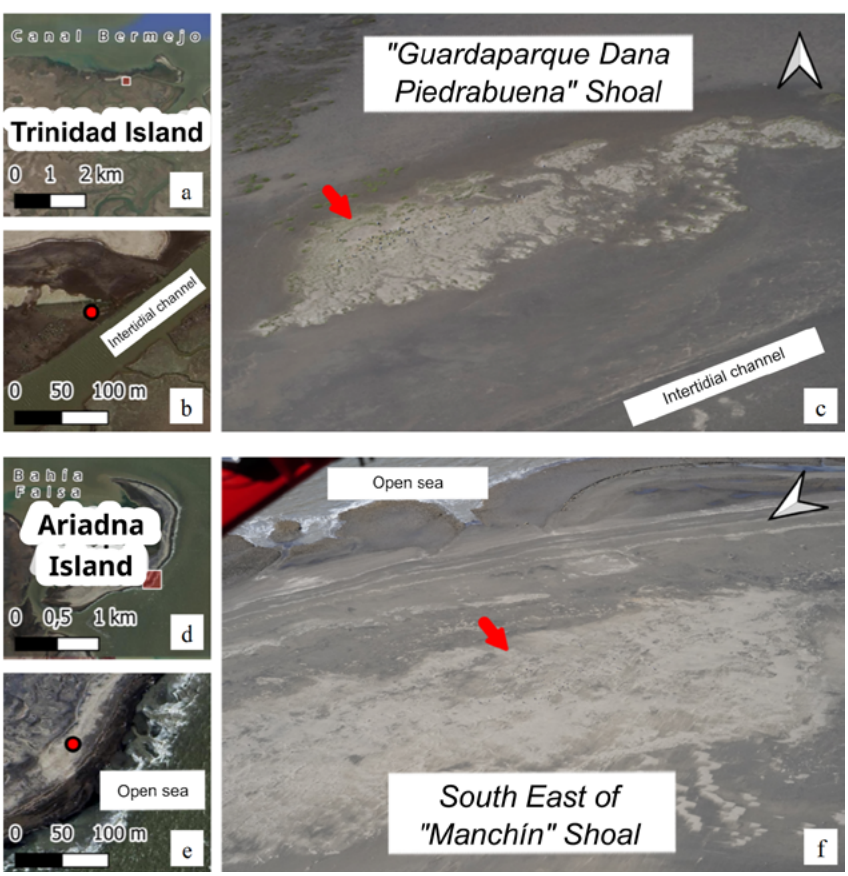


**Figure 3.** Aerial photographs of the new Olrog's Gull (*Larus atlanticus*) colonies reported on A–C) Trinidad Island and D–F) Ariadna Island (Buenos Aires, Argentina). The reference satellite images on the left (obtained from Google Earth) show the exposure of both colonies to water due to their proximity to the tidal line. The photographs were taken at approximately 11:00 h, when the tide was rising, between low tide at 07:29 h (1.18 m) and high tide at 13:50 h (3.29 m; Servicio de Hidrografía Naval 2025).

remember her valuable contribution to the monitoring of Olrog's Gull during the breeding-season field campaign conducted on Trinidad Island in 2024.

This work was also supported and endorsed by the Protected Areas Directorate of the Ministry of Environment of Buenos Aires Province, which approved the work plan and provided valuable expertise for conducting the survey. The study was conducted under permit EX-2025-20819596-GDEBA-DGAMAMGP.

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