Mentesana, L., A. Amador, P. Amorim, K. Delhey, P. Diniz, R. Fraga, G. B. Mindlin, J. C. Reboreda, A. Schaaf, B. Tassino, and N. M. Adreani. 2024. Biology of the Rufous Hornero, from mechanisms to behavioral ecology: a potential Neotropical model species? Journal of Field Ornithology 95(4):2. https://doi.org/10.5751/JFO-00544-950402

Review and Meta-analyses

Biology of the Rufous Hornero, from mechanisms to behavioral ecology: a potential Neotropical model species?

Biología del Hornero, de los mecanismos a la ecología del comportamiento: ¿una potencial especie modelo neotropical?

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ABSTRACT. Model organisms help us understand biological processes and provide insights applicable to other organisms. Birds are commonly used as model organisms. However, since most information comes from songbirds in the Northern Hemisphere, this limits our understanding of broader biological processes. Here we review existing knowledge on the biology of the Rufous Hornero (*Furnarius rufus*), a non-songbird found in southern South America. We highlight recent advances in research on its nesting, breeding behavior, and vocal communication, and propose promising new research questions. Finally, we discuss the potential of the hornero as a Neotropical model bird species.

RESUMEN. Los organismos modelo nos ayudan a comprender los procesos biológicos y proporcionan conocimientos aplicables a otros organismos. Las aves se utilizan habitualmente como organismos modelo. Sin embargo, dado que la mayor parte de la información procede de aves cantoras del hemisferio norte, esto limita nuestra comprensión de procesos biológicos más amplios. Aquí revisamos los conocimientos existentes sobre la biología del Hornero (*Furnarius rufus*), un ave no canora que se encuentra en el sur de Sudamérica. Destacamos los avances recientes en la investigación sobre su nidificación, comportamiento reproductivo y comunicación vocal, y proponemos nuevas y prometedoras cuestiones de investigación. Por último, discutimos el potencial del Hornero como especie modelo de ave neotropical.

Key Words: *behavior; birds; ecology; evolution; Furnariidae; Neotropics; suboscine*

INTRODUCTION

A substantial portion of knowledge in biological research stems from the study of model organisms: organisms that are extensively studied to provide generalized insights into biological phenomena. Although this approach has yielded remarkable success across different research areas, a lack of diversity in model organisms can also introduce bias in interpreting diverse biological processes. Scientific knowledge exhibits a clear geographical bias, likely attributed to geographical disparities across biological research fields rather than model species per se. Most studies in evolutionary biology and ecology originate in the Northern Hemisphere (Nuñez et al. 2021, Theuerkauf et al. 2022, Soares et al. 2023). Considering the differences in evolutionary forces and environments across hemispheres or continents, it is fair to assume that generalizations drawn from Northern Hemisphere research are unlikely to hold universally (Kennedy et al. 2017). Hence, efforts to establish new model species in underrepresented regions, such as the Neotropics (Mexico to Argentina and Chile), and within less-studied taxa become worthwhile, despite the challenges involved (Kennedy et al. 2017). Adopting an organismal approach in these regions can significantly enhance our understanding of diverse biological phenomena, spanning ecological to mechanistic (i.e., proximate causes) perspectives.

Birds have been used as models in disciplines ranging from neuroscience to evolutionary biology. For instance, Canaries (*Serinus canaria*) and Zebra Finches (*Taeniopygia guttata*) gained recognition as models for vocal learning and vocal production in neuroscience, among other fields (e.g., Goldman 1998, Griffith and Buchanan 2010). Similarly, Pied Flycatchers (*Ficedula hypoleuca*), Blue Tits (*Cyanistes caeruleus*), and Great Tits (*Parus major*) became pivotal models for behavioral ecology (e.g., Gibb 1950, Lundberg and Alatalo 2010). Despite the great diversity of birds in South America, only a handful of species have attained model status in ornithology (Soares et al. 2023). One of the most notable is perhaps the widely distributed Rufous-collared Sparrow (*Zonotrichia capensis*), important for the fields of behavioral endocrinology, behavioral ecology, or the study of vocal dialects (e.g., Miller and Miller 1968, Nottebohm 1969, Moore et al. 2002, 2004). Other songbirds that have the potential of becoming model species include the Shiny Cowbird (*Molothrus*

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bonariensis) and the Blue-black Grassquit (*Volatinia jacarina*), serving as models in brood parasitism and sexual selection, respectively (e.g., Mason and Rothstein 1986, Cavalcanti and Pimentel 1988, Sackmann and Reboreda 2003, Macedo and Manica 2019). Interestingly, all the examples here share a common trait: they all belong to the suborder Passeri, a group of around 5000 species.

The sister group of Passeri comprises the suborder Tyranni, consisting primarily of a Neotropical radiation of over 1000 species. Tyrannids, representing 26% of Passeriformes, are different from Passerids in, for example, life-history traits, neuroanatomy, and vocalizations (Gahr 2000, Liu et al. 2013, Oliveros et al. 2019). Among the several studies on Tyrannids, only one species appears to have achieved the status of an animal model: the Thorn-tailed Rayadito (*Aphrastura spinicauda*). Extensively studied, primarily in Chile, the rayadito provides essential insights into the biology of suboscines (e.g., Ippi et al. 2011, 2013, Botero-Delgadillo et al. 2017) and now serves as the primary outgroup for comparing discoveries in songbirds. However, given the enormous diversity within the Tyranni, it is evident that the Thorn-tailed Rayadito represents only a fraction of suboscine biological diversity. Because Tyrannids hold a more basal position in avian phylogeny, investigating more species will advance our understanding of avian evolution, including anatomy, neuroscience, life history, and more.

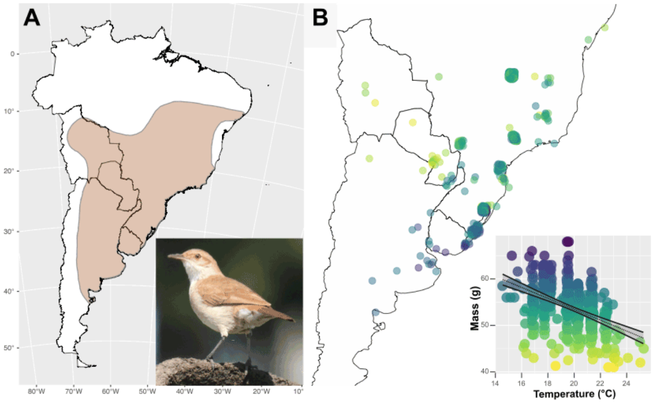
We review the knowledge on the Rufous Hornero (*Furnarius rufus*; hereafter referred to as the hornero), a Tyrannid of the Furnariidae family, widely distributed in southern South America and popularly known as ovenbirds. Since the first description of the species, and despite its popularity in the countries where it occurs (see Box 1), publications on the hornero have been sporadic with very few systematic approaches (e.g., Hudson 1923, Diesselhorst and Hermann 1958, Hermann 1958, Vaz-Ferreira and Palerm 1973, Fraga 1980). Only in the past decade different research groups in Argentina, Brazil, and Uruguay have, in parallel, initiated various research programs centering on horneros. This review aims to compile existing knowledge about these birds and inspire research on mechanistic, ecological, and evolutionary questions. We first present general aspects of hornero biology, then explore specific research topics, and finally, use the discussion to evaluate the potential of the hornero as a Neotropical model bird species.

General biology

Horneros are non-migratory and widely distributed in southern South America, in Argentina, Brazil, Bolivia, Uruguay, and Paraguay (Fig. 1A; Carman 1977, Remsen and Bonan 2020). They can be found in urban areas, savannas, pastures, and both agricultural and natural lands across the species distribution range (Remsen and Bonan 2020). The species is abundant and common where it occurs, it is classified as least concern, and its population appears to be increasing (BirdLife International 2023).

Horneros are relatively large ovenbirds, similar in size to the European Starling (*Sturnus vulgaris*; Fig. 1A). Depending on the population, they weigh between 40 to 70 grams (Fig. 1B). They have straight bills, rufous upperparts, and light rufous supercilia. The wings have a slight band, and their underparts are either brownish-grey or light cinnamon (Remsen and Bonan 2020).

Fig. 1. (A) Rufous Horneros (*Furnarius rufus*) inhabit Argentina, Paraguay, Uruguay, Bolivia, and Brazil. (B) Scatterplot depicting the association between annual mean temperature (from Fick and Hijmans 2017) and hornero body mass (r = -0.46, p < 0.001, N = 451, data from (Fraga 1980, Navas and Bó 1986, Schmitt et al. 1997, Oniki and Willis 1999, Bugoni et al. 2002, Di Giacomo 2005, Roper 2005, Aldatz 2006, Massoni et al. 2012, Smith et al. 2012, Salvador 2014, VerNet 2015a, b, 2017, 2018, 2019a, b, c, d, Rodrigues et al. 2019, Diniz 2024).



They exhibit minimal sexual dichromatism (Diniz et al. 2016, Barreira et al. 2021) and dimorphism (Aldatz 2006, Diniz et al. 2016), with females tending to be lighter colored and smaller than males. Moreover, horneros exhibit marked geographic variation in size: body mass negatively correlates with temperature variation following Bergmann's rule (Fig. 1B). This pattern is most likely driven by thermoregulatory factors, but a possible arms race with nest parasites could also contribute. Although predominantly insectivorous, horneros are known to feed occasionally on human food in urban areas and even prey on small vertebrates (Heredia et al. 2010, Miyasaki et al. 2017, Oliveira et al. 2022).

Both male and female horneros defend their territories year-round (Fraga 1980, Diniz et al. 2018). During the breeding season, horneros occupy large home ranges that vary from 0.7 ± 0.5 ha to 0.8 ± 0.3 ha. Territory sizes seem to decrease outside the breeding season, but it is unclear if this reduction is effectively in size or because horneros are less territorial (i.e., sing less or get less involved in territorial disputes; Amorim et al. 2023a). Both male and female horneros build the nest, which weighs an average of 4.30 kg and is made of mud (Fraga 1980, Massoni et al. 2012). Females lay 2–4 eggs in the austral spring and summer (i.e., September–February; Fraga 1980, Diniz et al. 2019, Rodrigues et al. 2019), with incubation and nestling phases lasting 14–18 and 23–26 days, respectively (Fraga 1980, Remsen and Bonan 2020). Both parents incubate and provide care (Fraga 1980, Massoni et al. 2012, Shibuya et al. 2015). Juveniles often remain in the natal territory for several months, delaying dispersal (Fraga 1980, Vaz-Ferreira et al. 1993, Bobato 2012). On average, pair bonds in horneros last three years (Fraga 1980, Amorim et al. 2023a). In a 12-year study on this species, males were 30% more likely to remain in a territory than females (Fraga 1980). This implies that either males have a higher likelihood of survival and/or changing partners than females, or females are more likely to die and/or abandon males while seeking new partners. However, in one population in Brazil, both sexes appear equally likely to keep their territories throughout the year (Amorim et al. 2023a). Furthermore, even though extra-pair paternity is widespread among socially monogamous birds (Brouwer and Griffith 2019), horneros appear to be an exception. The only available study suggests low extra-pair paternity in horneros, with 7% of broods and 3% of nestlings attributed to extra-pair males in an urban population in central Brazil (Diniz et al. 2019).

Behavior, physiology, ecology, and evolution

Hornero nest

Despite the attention nests have received in the fields of behavioral science, ecology, and evolution, numerous fundamental questions remain unanswered. A crucial step to understand behavioral, ecological, and evolutionary questions concerning animal architecture is to clearly identify and define different nest phenotypic traits so that they are replicable within one species and ideally generalizable to other bird species. This task can be exceptionally challenging, both in intricate and, especially so, in simple nests (e.g., Mainwaring et al. 2012). Bilateral asymmetry is a common binary phenotypic trait in nature, akin to handedness or the morphological asymmetry observed in certain crab species' claws (Palmer 2004). The simplicity of bilateral asymmetries makes them optimal traits for investigating the role of chance, environment, and genetics in explaining phenotypic variation (Palmer 2004). In this respect, hornero nests are bilaterally asymmetric (Fig. 2). Horneros construct nests with the entrance on either the left (Fig. 2A) or right (Fig. 2B) side of the dome, resulting in a clockwise or counterclockwise entrance to the incubation chamber. From a citizen science project that collected information on nest entrances in all five countries where the hornero is present, we now know that this trait is not randomly distributed in the population. There are 12% more nests with right entrances than expected by chance (Adreani et al. 2022). At present, it is challenging to discern a direct evolutionary advantage of one nest phenotype over the other; it could be that nest asymmetry is linked to another trait that may confer differential advantages (e.g., lateralized behavior) or simply unequally distributed in the population, like human handedness (discussed by Frasnelli and Vallortigara 2018). Additionally, large-scale environmental factors and nest site selection properties do not seem to account for the occurrence of left- or right-entrance nests (Adreani et al. 2022). Furthermore, the repeatability of this trait is among the highest reported for animal behavioral traits (R = 0.65), indicating that the likelihood of a pair building a new nest with the same asymmetry as the previous one is high (Adreani et al. 2022). This leaves two potential scenarios for explaining nest asymmetry: culture or genetics, which requires an experimental approach to be tested.

Because the hornero nest is primarily made of mud and the species originally evolved in central South America, it has been proposed to function as an incubation chamber when parents are absent (Vaz-Ferreira et al. 1992, Shibuya et al. 2015). The location and orientation of nests can also determine the thermal conditions inside the nest, influencing offspring development (Mainwaring et al. 2014, Martin et al. 2017, Schaaf et al. 2018) and potentially constitute key adaptive responses of species to the environment (Hartman and Oring 2003, Souza and Santos 2007, Mainwaring et al. 2014, Shibuya et al. 2015). Nest location and orientation are expected to be influenced by temperature, rainfall, humidity, wind, and nest materials among others (Conway and Martin 2000, Souza and Santos 2007, Schaaf 2020). In horneros, nests located closer to the Equator, where temperatures are high early in the breeding season (September and October) and rainfall is low, are often in areas with more vegetation or artificial cover (Schaaf et al. 2018). Nests without such cover tend to face south, likely to avoid direct sunlight and benefit from humid winds. The importance of climatic effects on hornero nest orientation is further supported by nesting records collected over 9 years from 7 sites in central Argentina. These records show a trend toward more southerly nest orientations as average temperatures increase (Schaaf and De la Peña 2020). Whether this trend helps reduce direct solar radiation or is a direct result of rising temperatures or other environmental factors (e.g., wind, changes in the landscape) remains an open question.

Most horneros build new nests every season, and those old nests can last for multiple years (Fraga 1980). This means that usable old nests become available for other bird species over time, such as many secondary cavity nesters. A survey of the literature revealed that hornero nests are used by at least 29 species of birds, belonging to 13 different families, mostly in the order Passeriformes (Fig. 2C; Delhey 2018). The most recorded secondary nest tenants include swallows, finches, house wrens, tyrant flycatchers, and New World blackbirds. Hornero nests are also used by invasive bird species such as House Sparrows (*Passer domesticus*) and European starlings (*Sturnus vulgaris*), with the former observed forcefully expelling the horneros from their nests (Fraga 1980). Interestingly, one bird seems to specialize in using hornero nests as their primary nesting site: the southern subspecies of the Brown-chested Martin (*Progne tapera fusca*). Although the northern nominate subspecies uses cavities, the southern subspecies nests almost exclusively in hornero nests (Turner 2020). In addition to birds, hornero nests are also used as roosting sites by mammals such as opossums, and bats, among others (Narosky and Carman 2008), and they contain associated invertebrate fauna (Turienzo and Iorio 2007). This includes ectoparasites such as hematophagous bugs (*Acanthocrios furnarii*, Cimicidae). Hence, by providing a key resource (nest sites) for other species, horneros may act as physical ecosystem engineers, that is, species that create new environmental resources with broad implications for ecosystem dynamics (Jones et al. 1994). Woodpeckers (Family Picidae) are well-known examples of avian ecosystem engineers (van der Hoek et al. 2017). However, in contrast with woodpeckers, horneros create cavities where woodpeckers cannot: on small trees, buildings, and other artificial substrates. In fact, horneros thrive in human-modified landscapes, and their nests could be the key element that attracts a diversity of other birds to these often-impoverished urban environments.

The hornero nest therefore offers a wealth of opportunities in three research areas: one avenue explores the asymmetric nature of the hornero nest as a pivotal phenotype, investigating the roles of genes and culture in nest architecture, aspects related to cognition, and the extent to which both males and females contribute to the asymmetry. A second avenue examines the ecology of nest site selection in relation to climate and explores

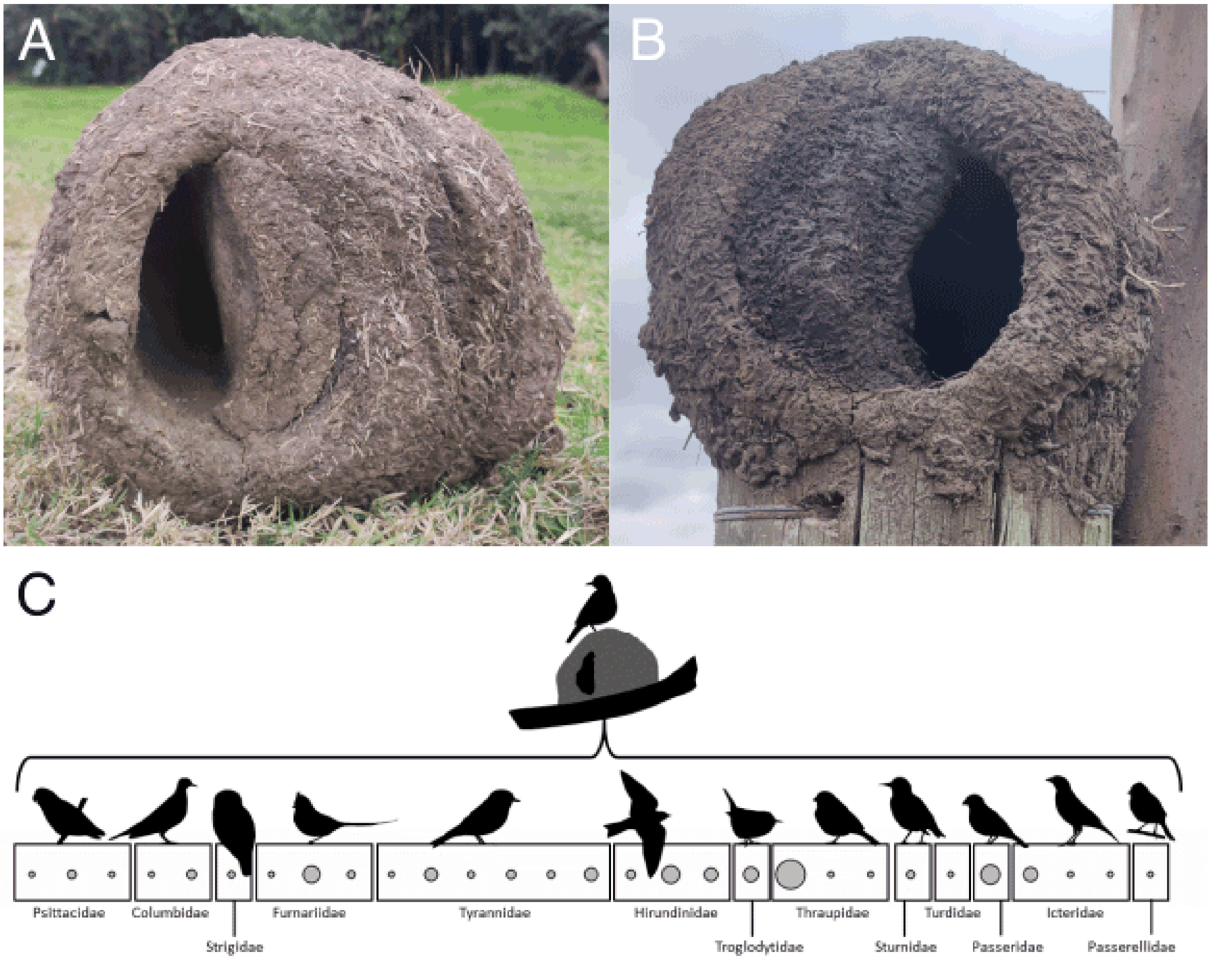


Fig. 2. The Rufous Hornero's (*Furnarius rufus*) nest is primarily built with mud, and its entrance can be (A) on the left or (B) on the right. (C) Hornero's nest serves as a cavity provider for different species of secondary cavity nesters. Silhouettes represent different families and within each family the circles represent species. The size of the circles is proportional to the degree of usage of hornero nests by the species following Delhey (2018).

the consequences of nest orientation on bird phenology, internal nest temperature, and birds' behavior and fitness. The third avenue focuses on the ecological importance of hornero nests in different environments and their putative role as ecosystem engineers. The conspicuousness of the nest and the wide distribution of the species in both rural and urban areas provide an excellent opportunity to address the last research question by involving the public. For example, citizen science initiatives could prompt people to observe hornero nests during the breeding season, quantify their longevity over several years, and record whether it is used by another species.

Breeding biology

Antiparasitic behavior: Brood parasitism reduces reproductive success of the host and selects for antiparasitic defenses and results in a coevolutionary arms race (Davies and de L. Brooke 1988, Davies 2011, Soler 2017). The most common antiparasitic defense is the rejection of parasite eggs, either by ejection or nest desertion and most hosts use differences in eggshell background color and spots between their own and parasite eggs to recognize and reject foreign eggs (Krüger 2007, Abolins-Abols et al. 2019).

The hornero is a host of the brood-parasitic Shiny Cowbird, but the frequency of parasitism varies widely within its distribution. In Argentina, it ranges from 2% of nests in Buenos Aires province to 59% in Formosa province, with intermediate values in Córdoba (13%) and Santa Fe (39%) provinces (De Mársico et al. 2010). In Uruguay, it is 44% (Tosi-Germán 2015). Horneros eject cowbird eggs by grasping them at the widest part (Mason 1986, Tosi-Germán et al. 2020). However, because of the darkened interior of the incubation chamber of its closed nest, cues based on eggshell color might not be useful for recognizing cowbird eggs under some climatic conditions. Mason and Rothstein (1986) proposed that horneros use differences in size to recognize and eject parasitic eggs.

In a study conducted in Uruguay, where Shiny Cowbirds frequently parasitize horneros, Mason and Rothstein (1986) demonstrated that horneros eject parasite eggs based on their width and length. They also showed that in Uruguay, Shiny Cowbird eggs are larger than those in Buenos Aires province, where horneros are rarely parasitized by Shiny Cowbirds. They proposed that this increase in egg size is a counteradaptation by cowbirds to evade the discriminatory cue used by horneros. There is also evidence of a coevolutionary arms race in Formosa, Argentina, where Shiny Cowbirds heavily parasitize horneros. In this region, horneros and Shiny Cowbirds are 25% and 10% smaller in body mass, respectively, than in Buenos Aires. As expected by allometry, the hornero eggs in Formosa are smaller than those in Buenos Aires. However, contrary to expectations, the eggs of Shiny Cowbirds in Formosa are larger than those in Buenos Aires. Horneros in Formosa eject Shiny Cowbird eggs with widths less than about 88% of the widths of their own eggs (as reported by Mason and Rothstein 1986 in Uruguay). However, because Shiny Cowbirds lay larger eggs than expected by allometry, horneros cannot discriminate between their own and most parasitic eggs, resulting in high levels of parasitism (Di Giacomo, Massoni, and Reboreda, *unpublished data*).

A study by Tosi-Germán et al. (2020) showed that horneros do not need to compare the parasite egg with their own eggs, which is consistent with the hypothesis of a template or mental image of their own eggs. The use of a template-based recognition mechanism has been reported in hosts that reject parasite eggs based on differences in background eggshell color or spotting (Moskát et al. 2010, Bán et al. 2013, Manna et al. 2017). However, the hornero would be the first host that ejects parasitic eggs using a template-based recognition mechanism for the size of their eggs. In this species, both sexes eject cowbird eggs. In hosts where females incubate alone, they are responsible for egg rejection (Palomino et al. 1998). Still, if incubation is shared, as in horneros, males may also eject parasitic eggs (Soler et al. 2002, Lee et al. 2005). The ejection of parasitic eggs by males and the use of a template or mental image to discriminate between their own and foreign eggs imply that males should learn the characteristics of their partners' eggs. By studying horneros we can gain knowledge on the cognitive processes underlying the evolution of female and male antiparasitic defenses, how these defenses may drive the evolution of parasite counter-defenses, and how selection for certain life history traits, such as body size, may constrain or facilitate coevolutionary processes between hosts and parasites.

Aggressive behavior: Elaborate and costly traits, like agonistic behavior, found in both males and females have been shown to result from social competition for ecological resources, like territories (West-Eberhard 1983, Kraaijeveld et al. 2007). In such cases, individuals should benefit from displaying ornamented and conspicuous traits outside breeding contexts, and selection pressures are expected to be balanced between the sexes. At present, the roles of sexual and nonsexual competition are both recognized as important selection factors acting on the expression of costly traits. Yet, the extent to which each of these selection pressures shapes elaborate traits remains an open question, partially explained by the geographic bias in ornithological studies, which are more common where males are typically more ornamented than females (e.g., Kraaijeveld et al. 2007, Tobias et al. 2011).

The hornero may be a key species for addressing evolutionary questions about presumably costly traits present both in males and females. As explained above, male and female horneros defend their territory year-round (Fraga 1980, Diniz et al. 2018), often for multiple years (Fraga 1980, Amorim et al. 2023a). Remarkably, in two breeding contexts (mating and provisioning), the same set of behaviors explained how male and female horneros defend their territory, with number of flights over the decoy and duets being the best predictors of territorial defense (Mentesana et al. 2020). Moreover, aggressive interactions (e.g., fights or displacements) and duets are also important behaviors performed by both sexes when defending their territory outside the breeding season (Diniz et al. 2018, 2020). Although in some populations, males are more aggressive than females when defending their territories throughout the year (Diniz et al. 2018, Mentesana et al. 2020), Diniz et al. (2020) and Amorim et al. (2022, 2023b) observed that aggression levels are similar in both sexes. Aggressive behavior in horneros seems to be influenced by social competition for territories. This is supported by their year-round territoriality, shared territorial defense behaviors, and in some populations, equal aggression in both sexes (Diniz et al. 2019).

The field of bird physiology has predominantly focused on males (as reviewed by Caro 2012, Kimmitt 2020, Smiley et al. 2022), mirroring the existing trend in behavioral ecology. This bias persists in current literature, with 82% of studies involving male birds, 61% involving females, and only 43% considering both sexes (reviewed by Kimmitt 2020). Consequently, there is a significant gap in understanding the physiological mechanisms underlying female behavior. For instance, over the past 30 years, researchers have developed a conceptual framework elucidating the role of the steroid hormone testosterone in modulating social behaviors, such as territory defense, in males (known as the "challenge hypothesis"; Wingfield et al. 1990). The lack of experimental support for the "challenge hypothesis" led to the recent proposal of a modified version ("challenge hypothesis 2"; Goymann et al. 2019). In contrast to males, our understanding of steroid hormones in mediating social behaviors in females is in its early stages. Importantly, the framework used for investigating such questions is not specifically tailored for females but rather follows the framework designed for males (discussed by Smiley et al. 2022).

To understand the mechanisms mediating territorial defense in males and females, Adreani et al. (2018) and Mentesana and Adreani (2021) experimentally studied if and how steroid hormones modulate territorial defense in horneros during the breeding season. In response to a territorial intrusion, neither males nor females changed their testosterone levels, but only males increased their progesterone levels. Moreover, Mentesana and Adreani (2021) studied if both sexes experienced similar physiological consequences from aggression. Here, aggressive interactions decreased the concentration of antioxidants (molecules that protect tissues from oxidative damage) in both males and females. However, females experienced a more abrupt decrease compared to males. Interestingly, while in the experimental group, more aggressive females had lower antioxidant levels than less aggressive ones (a sign of causation); this was not the case for males. Altogether, these results suggest that defending territories in horneros could be modulated differently in males and females, despite both sexes performing the same set of behavioral responses during such interactions. And that engaging in aggressive interactions might have different physiological consequences for males and females: females experience a higher exposure to oxidative stress compared to males when being aggressive. Whether this difference in antioxidant levels affects females' fitness is yet to be determined. If it does, it could explain why female horneros are often less aggressive than males.

Hence, horneros can be a valuable species to examine the contribution of sexual and nonsexual selection pressures to the evolution of agonistic behavior, as well as the physiological mechanisms underlying it. Horneros can enhance our understanding of whether certain hormones function similarly in both sexes, identify unique mechanistic differences, and shed light on factors influencing physiological responses in males and females.

Vocal communication

Mechanisms of vocal production

Songs are important correlates of fitness because they are used for mate attraction, territorial contests, and other reproductive behaviors. Given their vocal diversity and the beauty of their songs, Passeriformes are possibly the most studied group in terms of vocalizations. Within this order, songbirds (Passeri) are vocal learners, and the complexity of their songs is due to the richness of neuromuscular control (Amador et al. 2017). Non-songbirds (Tyranni) are generally not considered to be vocal learners, and, for this reason, they are very much understudied compared to oscines. However, suboscines produce a rich variety of songs with a great degree of complexity including perceivably intricate duets, raising the question of which mechanisms allow such flexibility without learning.

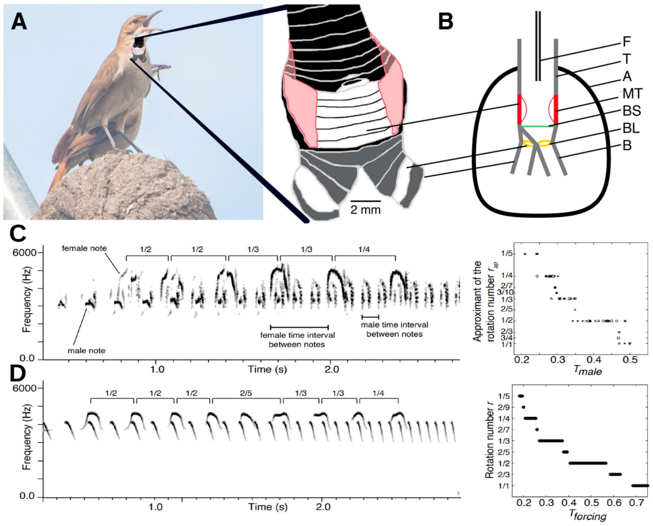
To understand Tyranni vocal complexity, its diversity, and the evolutionary processes underlying it, the central nervous system, the peripheral nervous system, and the anatomy of the syrinx must be studied. Tackling each of these systems involves numerous challenges, but a solid starting point lies in understanding the anatomy and its relationship with the sound produced by the birds. This approach has two advantages: the measurability of anatomy and the ability to model the dynamics of sound production. Based on anatomy and thanks to advancements in linear and non-linear dynamics, we understand how songs are produced. Birdsong production involves the emergence of complex and coordinated rhythms that can result from non-linear physical processes (Mindlin 2017). A straightforward example is the oscillation of tissues, such as syringeal membranes or labia (depending on the species), when airflow passes between them. These oscillations modulate airflow, resulting in sound production (Mindlin and Laje 2005). Interestingly, both the oscillations of the syringeal tissue and the neuronal activity responsible for respiratory rhythms have nonlinear characteristics. Consequently, in both cases, a diverse range of non-trivial effects acoustically and rhythmically shape the song. Mathematical modeling plays a crucial role in this context, as sophisticated dynamical models enable precise predictions regarding the potential interactions between the central nervous and peripheral systems, which contribute to the observed songs. Thus, with appropriate dynamic models, it is possible to reverse-engineer the different mechanisms of vocal complexity.

Horneros, and other suboscines, are tracheophones: they possess a syrinx with a pair of membranes (one ventral and one dorsal), above the point where the bronchi meet and merge into the trachea (Figs. 3A and B; membrane tracheales [MT]). Initially, because of anatomical considerations (Rüppell 1933), these membranes were believed to be the primary sound source for these species, hence the name "tracheophones." However, Garcia et al. (2017) showed that vocal production includes three sound sources. In addition to the MT, a pair of opposing bronchial labia (BL; resembling the labia in the well-studied oscine syrinx) is located at each juncture of the bronchi and the trachea (Figs. 3A and B). In six suboscine species, including horneros, fiberscope examination showed that the intact syrinx could produce pulse-like signals (Garcia et al. 2017). When MT were non-functional, the pulsatile nature of the oscillations ceased, leading to a decrease in sound amplitude and an increase in oscillation frequency. Notably, these were not only present in the induced vocalizations of anesthetized animals but also in the distress calls of several studied species. Beyond the direct description of experimental manipulations, all findings were successfully replicated through a dynamical system model. This model was designed to characterize oscillations associated with both MT and BL, assuming synchronization between the two bronchial sound sources. All experimental outcomes could be reproduced by this dynamical model, which also created realistic synthetic sounds (see Garcia et al. 2017 for details). More remains to be investigated, for example, the study of the biological importance of these rough sounds or the role of the three vocal sources in natural songs and duets.

Songs can be produced by one individual as well as jointly by several individuals in a duet or chorus manner (Farabaugh 1982, Langmore 2002, Hall 2004). Horneros produce highly structured duets with sex-specific contributions (Laje and Mindlin 2003, Amador et al. 2005, Roper 2005). During a duet, males generally initiate their vocalizations with a note production rate of approximately 6 Hz and gradually increase their note rate by roughly 200%. The temporal evolution of female note production rate is more variable, yet the timing remains structured. To quantify this synchronization pattern, and to generate predictions about the underlying mechanisms of duet synchronization, Laje and Mindlin (2003) modeled the duets as a system of externally forced oscillators. Linear oscillators tend to synchronize with the forcing signal, whereas nonlinear oscillators can have a range of locking regimes. Hornero duets have an intricate rhythmic behavior that is effectively represented by the stair-like pattern, a well-known phenomenon in the literature referred to as the "devil's staircase" (Figs. 3C and D). It commonly occurs when periodically forcing either a nonlinear oscillator or an excitable system (Bak 1982).

The presence of this specific signature of nonlinear behavior was interpreted as the result of male notes acting as a driving force on the female motor system through the auditory pathway. This hypothesis was tested in a dynamic system model that reproduced the observed behavior (Figs. 3C and D; Laje and Mindlin 2003)

Fig. 3. Rufous Hornero (*Furnarius rufus*) vocal organ and duet dynamics. (A) A drawing of a ventral view of the hornero syrinx, where the syringeal muscles are colored in pink. (B) Schematic of a lateral view of the tracheobronchial junction. F, fiber optic cable; T, trachea; A, air sac; MT, membrana trachealis; BS, bronchial septum; BL, bronchial labia; B, bronchus. (C) Left panel: spectrogram of a hornero's duet. The locking sequence between male and female vocalizations in this duet is shown above the spectrogram (rotation numbers). Right panel: approximation of the rotation number as a function of the normalized average time interval between male notes (N = 11 hornero duets). (D) Left panel: spectrogram of a synthetic duet. Right panel: rotation number as a function of forcing period, for a nonlinear oscillator subjected to periodic forcing. This steplike organization is known as the devil's staircase. The bottom axis is normalized to the natural period of the driven oscillator.



and generated testable predictions for the female respiratory activity during the duet (Amador et al. 2005). However, despite some isolated efforts (Liu et al. 2013), the suboscine neural structures remain largely unexplored, presenting a fascinating animal model that exhibits highly complex and rich behavior. Finding the neural substrate responsible for this complex rhythmicity would be a starting point for unveiling the sensorimotor integration in birds that presumably lack vocal learning capacities.

The function of duets

Duets occur in approximately 16% of bird species, are taxonomically widespread, and have evolved multiple times (Tobias et al. 2016). They seem to have several functions, including joint territory defense and mate guarding (Hall 2004, 2009, Dahlin and Benedict 2014, Tobias et al. 2016). Understanding duetting is key to gaining knowledge on the evolution of female songs, communal vocalizations, and cooperation in social species. Yet, compared to solo songs, duets are least understood, which might be partially explained by duetting species occurring mostly in tropical and subtropical habitats (Tobias et al. 2016).

In the hornero, partners overlap 60% of their sex-specific songs in a loud ~8-second duet (Diniz et al. 2018) and their duets possibly propagate over long distances (Amorim, Guaraldo, and Diniz, *unpublished manuscript*). Although both sexes produce solo songs, males predominantly lead the duets and are more responsive to partner-initiated songs (Roper 2005, Diniz et al. 2018). Song answering and duet production responds to territorial intrusions year-round and peaks during pre-breeding and juvenile dispersal stages, respectively (Diniz et al. 2018, 2020, Mentesana et al. 2020). Female song signals territory quality and duet duration is positively related to fledgling success (Diniz et al. 2019). These studies indicate that duets signal year-round territorial defense and may also act as mutual mate guarding and acoustic paternity guarding by males during the female fertile period (Hall 2004, Dowling and Webster 2018).

Playback studies confirm the duet functions in horneros. Partners coordinate responses similarly to both paired and solo intruders, with an 80% song overlap and correlated physical and vocal responses (song rate and duration) between partners (Diniz et al. 2020, Mentesana et al. 2020). Females respond more to female intruders, suggesting that mate guarding drives female song and territoriality, with males cooperating in deterring female intruders (Diniz et al. 2020). Additionally, these birds show caution when responding to duets with a higher degree of song overlapping and tend to respond with more overlapping songs to playbacks of duets that are rhythmically coordinated (Diniz et al. 2021). This suggests that duet coordination encodes information about coalition quality of partners in territory defense (Hall and Magrath 2007). A recent study by Amorim et al. (2022) suggests that both sexes can also differentiate between neighbors and strangers through their duets. However, it is unclear if this ability is selected in both sexes and if there is cooperation with the sex that distinguishes the duet (Amorim et al. 2022).

In summary, horneros may duet to cooperatively defend their territories, guard mates, and signal coalition quality (Diniz et al. 2018, 2020, 2021, Mentesana et al. 2020). Future research could explore additional roles of duetting in this species, like promoting behavioral coordination and spatial cohesiveness between partners (Logue 2007), confirming partner identity (Kunkel 1974, Hall 2004, 2009), or encoding qualities related to fighting outcomes (Smith 1994, Hall 2004, 2009). Investigating male duetting in preventing extra-pair paternity through male removal experiments is also important (Dowling and Webster 2018). These findings highlight the complexity of acoustic signals in tracheophone suboscines and their role in duet evolution among birds.

Box 1. Hornero's cultural importance and its potential as a charismatic species.

In every country where they occur, Argentina, Bolivia, Brazil, Paraguay, and Uruguay, horneros are emblematic species. In general, because of their conspicuous nests and nest-building activities, horneros symbolize hard work, intelligence, joy (because of their duet singing), and fidelity (because of their monogamous system). Moreover, this bird is deeply rooted in the culture of every country where it occurs, and multiple legends exist about it. In Argentina, the hornero is the national bird, chosen by primary school students in 1928 (Villafuerte 1962).

Also in Argentina, closed hornero nests have been associated with the burial of the deceased partner or the entombment of nest usurpers such as house sparrows (Carman 1973, *unpublished manuscript*). In Bolivia, there are even records of hornero nests being used for medicinal purposes (Paca Condori, *personal communication*). In this case, the mud extracted from a nest built on a Peruvian pepper tree (*Schinus molle*) is applied to the face to treat facial paralysis, and tobacco smoke blown into the hornero nest is used to cure people with ear pain (Paca Condori, *personal communication*). Narosky and Carman (2008) also mention similar applications in the northwest part of Argentina. In Brazil, legend has it that if one member of a hornero pair cheats, the other will close the nest using mud with the partner inside (de Almeida 2003). Although these stories are highly implausible, such closed nests do exist (Delhey, *personal communication*), but as far as we know have not been examined. In Brasília, the capital of Brazil, the satellite city of Sobradinho ("house with two floors") gets its name from hornero nests with a distinctive feature: the overlapping of nests in a single location, situated at the entrance of the city (Neto 1998). In Paraguay, the Guaraní legend suggests that a couple of potters who did not have their blessings to get married were killed after insisting on it and then transformed into horneros (Yampey 2003). Not all cultures consider horneros favorably. Florian Paucke, a Jesuit monk, recorded that the Mocovi in the Chaco region would throw rocks at horneros and destroy their nests because the bird was suspected of disclosing private conversations to others (Carman 1977). The popular allure of the hornero is also reflected by the fact that horneros often feature in poetry and music (Villafuerte 1962; Narosky and Carman 2008). For example, the horneros have been a topic in the songs of influential songwriters like Atahualpa Yupanqui, Alfredo Zitarrosa, Maria Elena Walsh, and Maria Gadú.

All these examples of the hornero's cultural relevance demonstrate that in general humans have a lot of empathy toward the species, almost everyone can identify the bird and, even more easily, their nest. This presents great potential for the use of this species, not only for the development of citizen-science projects involving the species (e.g., Adreani et al. 2022), but also as a "flagship" species in outreach and science communication.

DISCUSSION

We have reviewed several ongoing and foundational research lines concerning the hornero. A key question arises: Is the hornero a good model species? Model organisms can be defined in two ways: as a "multi-purpose" species, thoroughly researched to understand various biological phenomena, or as a "topic-specific" species, optimal for studying a particular process or system (Leonelli and Ankeny 2013). We believe the hornero has potential as both a multi-purpose and a topic-specific model species.

To qualify as a multi-purpose model, a species should (i) be accessible, easily observable, and individually identifiable; (ii) possess traits of interest across different research fields; (iii) tolerate experimental manipulations; and (iv) allow extrapolation to other animal systems. Regarding (i), horneros are widespread, with conspicuous and accessible nests that resemble natural nest boxes. They can be easily captured and individually marked with color rings. For (ii), the accessibility of nests allows for the study of fitness traits like clutch size and fledging success. Additionally, horneros are territorial, long-lived, and have adapted to urban environments, facilitating diverse research questions such as: ecological drivers of territoriality and its link to urbanization, the relationship between longevity, territory quality, and reproductive success, behavioral mechanisms and ecological drivers of cooperation in parental care or nest building, and their role as cavity providers for the avian community, among others. Their long lifespan and year-round territoriality also support long-term population monitoring and investigations at individual and population levels. For (iii), horneros offer ample opportunities for experimental manipulation, such as altering clutch size, thermal properties of the nest, social composition, or population density. Finally, for (iv), many aspects of hornero biology are relevant to other bird species and taxa. For example, findings on cavity-nesting behavior and territoriality can be applied to other species, including woodpeckers and urban-adapted birds.

To be a topic-specific model, a species must have unique features that make it ideal for studying a specific topic. For horneros, their distinctive nest-building behavior stands out. Although nest building is common in birds, its complexity and quantification remain challenging. Horneros build unique, conspicuous nests, and their nest-building behavior can be precisely studied in the wild. Thus, horneros could serve as a model for understanding nest-building behavior and animal architecture. Questions such as how pairs coordinate nest building, the representation of nests in the birds' brains, the repeatability of nest-building behavior, and the behavioral mechanisms behind nest architecture are particularly relevant. Horneros could provide unique insights into these aspects of nest-building behavior.

CONCLUSION

It is now generally accepted that our global understanding of nature is hindered by a deep geographical bias toward Northern Hemisphere species. One way to overcome this is to establish long-term research lines in underrepresented species and position them as comparable models to those already established. By doing so, we will be able to disentangle patterns that are common to birds in general from taxon-specific ones driven by the specific evolutionary history of certain species.

This review highlights foundational research lines, and three promising areas focused on mechanistic, ecological, and evolutionary questions related to nest traits, breeding, and singing behavior. Additionally, given the species' relevance in its native countries, horneros are valuable for research using citizen science and for strengthening the relationship between science and society. Establishing horneros as a model species will depend on the consistency and continuity of current research lines as well as the development of new ones.

As a starting point, we have established the Furnarius Research Network (FuRNet). FuRNet is a collaborative and open network of scientists based in Argentina, Uruguay, Brazil, and abroad who have worked and are currently working with the hornero. We present different research lines and interests, as well as remaining open to questions and future directions. We hope that this review serves as motivation not only for South American ornithologists and students to become interested in investigating this species, but also for ornithologists in general to consider the possibility of addressing research questions on these amazing birds.

Author Contributions:

All authors conceived, discussed, and wrote sections of the original draft. NA analyzed the data on horneros renesting in the same territory over years, and KD tested the Bergmann's rule. LM and NA reviewed and edited the draft.

Acknowledgments:

We thank the Editor and two anonymous reviewers for their constructive feedback, which greatly improved our manuscript.

Data Availability:

All data and code are available on Open Science Framework: https://doi.org/10.17605/OSF.IO/6Q2XD

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