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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 &

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Collias 1986, Hansell 2005, Martin et al. 2017). For example, nesting sites in urban locations include 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.

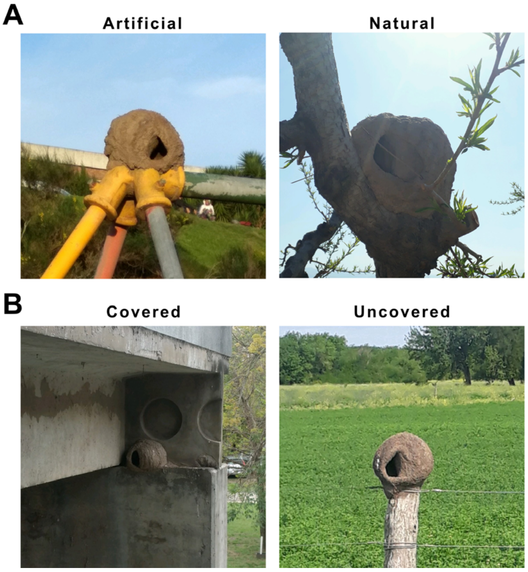

Figure 1. Examples of two Hornero (*Furnarius rufus*) nest site characteristics reported by citizen scientists across natural, rural and urban areas in Argentina, Bolivia, Brazil, Paraguay, and Uruguay: (A) nest substrate type (i.e., if the nest was built on a natural or artificial, human-made structure), 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: $n_{\text{artificial}}$ = 3364, n_{natural} = 1774; urban: $n_{\text{artificial}}$ = 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).

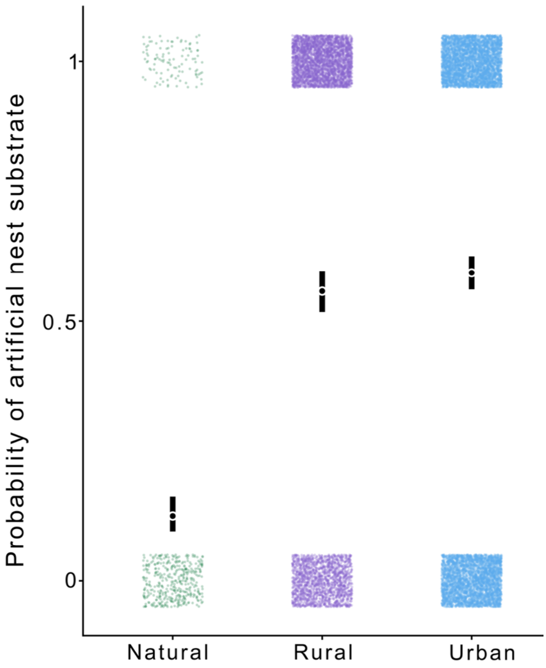

Figure 2. Nest site substrate (0 = if built on a natural structure; 1 = if built on an artificial, human-made structure) of horneros (*Furnarius rufus*) reported by citizen scientists across natural, rural, and urban areas in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Colored dots represent the 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 σ^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

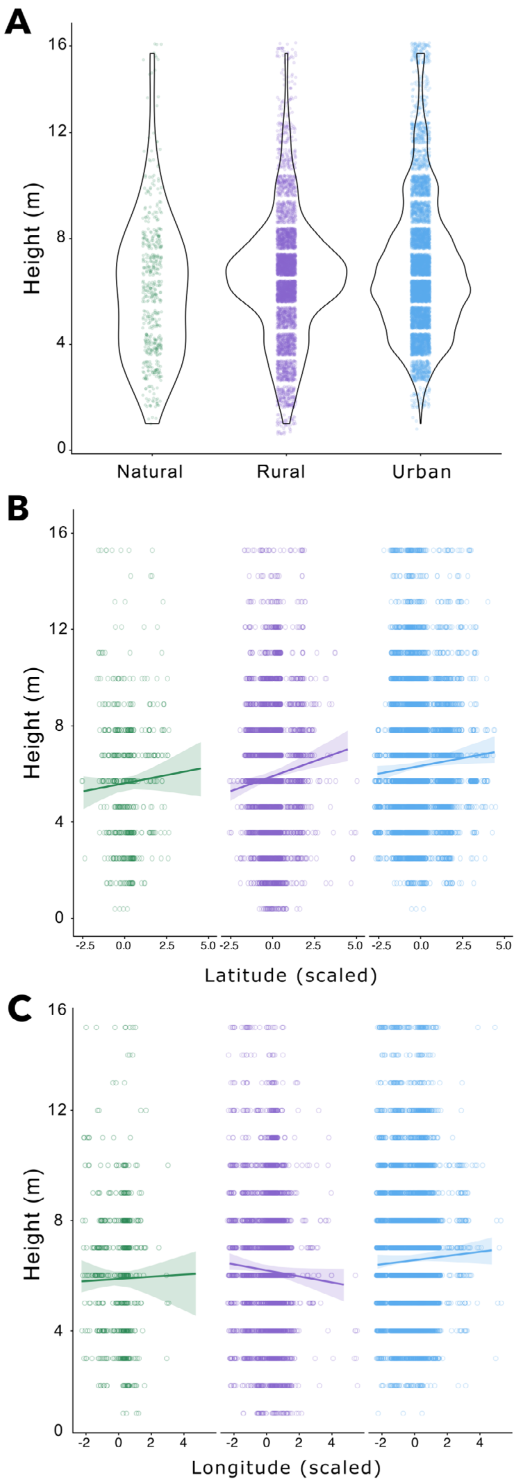

Figure 3. Nest height (i.e., meters of the nest above the ground) of horneros (*Furnarius rufus*) reported by citizen scientists across natural, rural, and urban areas in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Colored dots represent the raw data for natural (green), rural (purple) and urban (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 σ^2 (95% CrI)	
User ID	2.808 (2.641; 2.978)	2.904 (2.720; 3.098)
Residual	4.340 (4.235; 4.445)	-

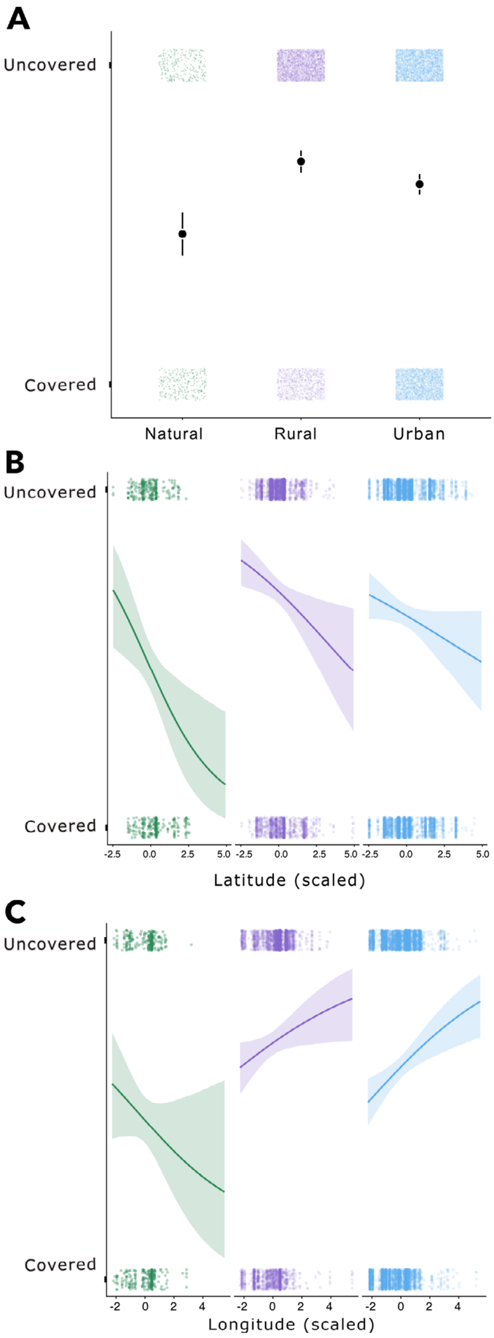

Figure 4. Nest cover (i.e., whether the nest was covered or not by either a natural or artificial structure) of horneros (*Furnarius rufus*) reported by citizen scientists across natural, rural, and urban areas in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Colored dots represent the raw data 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).

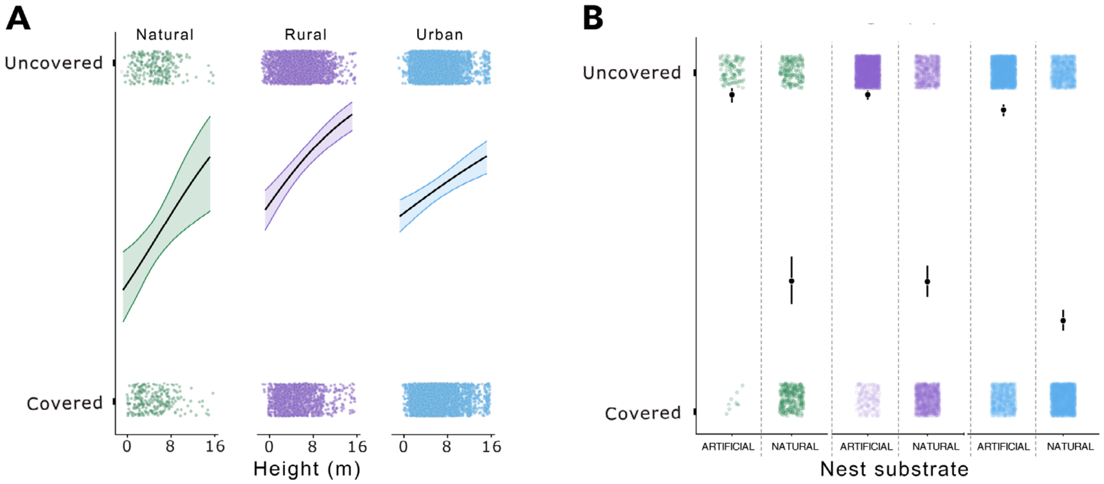

Figure 5. Relationship between Hornero (*Furnarius rufus*) (A) nest height (i.e., meters of the nest above the ground) and (B) nest substrate (0 = if built on a natural structure; 1 = if built on an artificial, human-made structure) with the probability of nest cover (i.e., whether the nest was covered 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)	
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 σ^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, CS 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 et al. 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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