Correspondence

Asymmetric architecture is non-random and repeatable in a bird's nests

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Bilateral, or left–right, asymmetry has evolved independently in many life forms and can be randomly, genetically or environmentally determined[1]. In a population, the frequency of left and right phenotypes can vary randomly or be fixed depending on, for example, their adaptive value[1]. Bilateral asymmetry has been described and quantified in individual morphological or behavioral traits, such as internal organ asymmetry or handedness[1–3], but rarely in extended phenotypes. Bilateral asymmetry is present in animal architecture, such as snail shells or bird nests. How common and important asymmetry is in animal architecture remains to be quantified[4]. Here, we use a citizen-science approach to quantify the occurrence of left–right asymmetry in the complex nest of a bird, the rufous hornero (*Furnarius rufus*). We assess the possible evolutionary mechanisms underlying asymmetric nest architecture and predict a genetic underpinning.

Male and female horneros contribute equally to building a 'clay-oven' mud nest, with the entrance on either the left or the right side (Figure 1A,B)[5,6]. We collected data from 12,606 nests throughout the species' entire range (ca. 4,8 million km[2]; Figure 1C). Using a smartphone application, citizen scientists collected data on nest asymmetry, nest site properties (height, cover, substrate, entrance cardinal orientation and urbanization context) and photographed the nest. Based on the nests' GPS locations we also collated a dataset of large-scale environmental variables (i.e. temperature, precipitation, and altitude). Horneros pair for life and defend their territory year-round, and although a nest can last several years birds do not reuse it across seasons[6]. Thus, nests from consecutive breeding seasons can be found in one territory, allowing repeated measures of nest asymmetry from the same pair (Figure 1E).

At the population level, we found 12% more right-entrance nests than left-entrance nests, which differed from random expectation (Figure 1D; $P_{(dif)} > 99.99\%$ for the comparison right-entrance mean estimate [95% Credible Interval (CrI)] = 0.56 [0.55–0.57] vs. Random mean estimate [95% CrI] = 0.50 [0.48–0.52]; n= 12,606; Supplemental

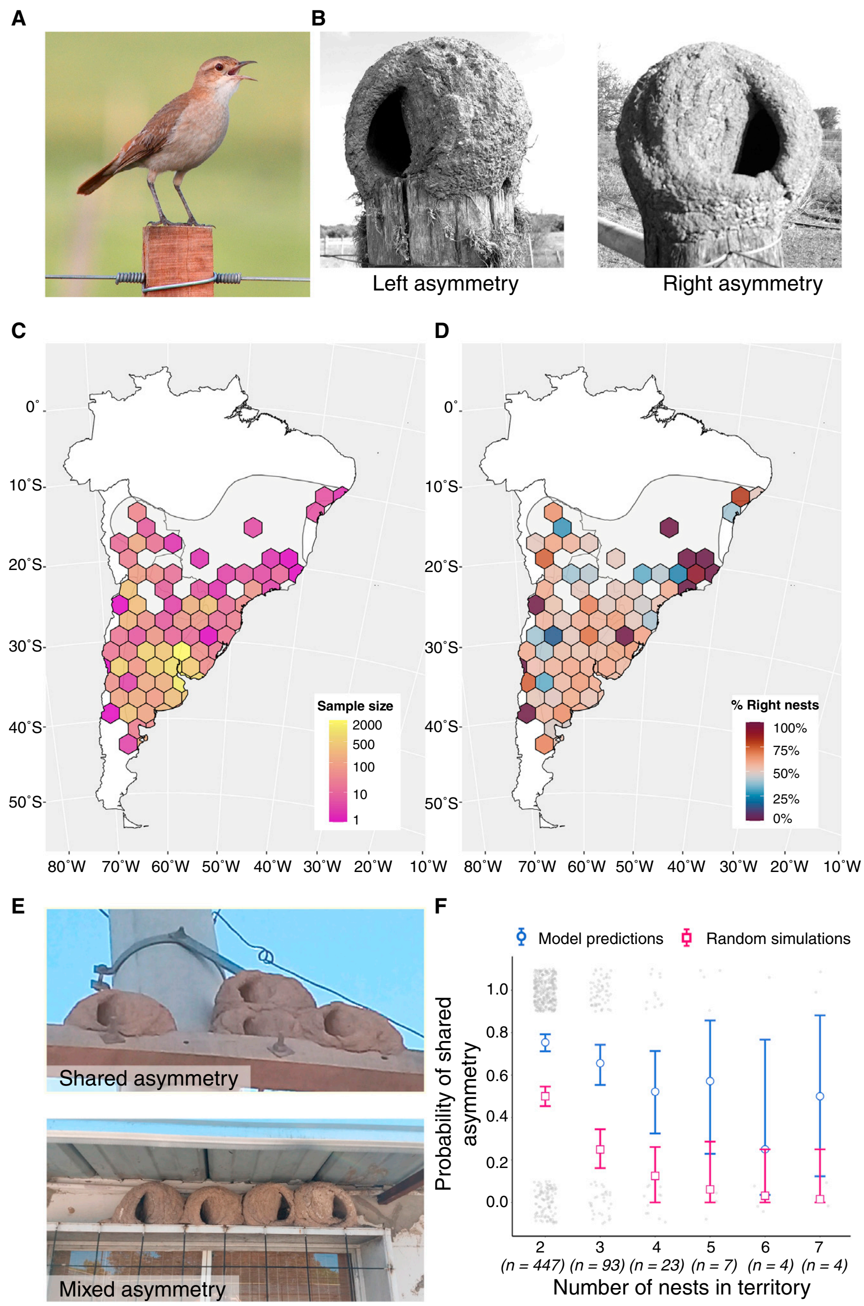

Figure 1. Horneros' 'clay-oven' mud nests have a bilaterally asymmetric architecture.
(A) Rufous hornero (*Furnarius rufus*). (B) Left- and right-sided nests. (C) Total sample size and (D) proportions of right-sided nests. The shaded grey area represents the breeding range of the rufous hornero. (E) Examples of shared- and mixed-asymmetry territories. (F) Probability of shared asymmetry (blue circles) within a territory compared to a random-probability model (pink squares) for territories with different number of nests (2–7; n = 544 territories). Colored shapes represent the mean estimates and vertical bars the 95% credible intervals. Grey circles are the raw data.

information). Bilateral asymmetry in horneros' nests possibly originated as a random trait[1]. At present, it could be a case of directional asymmetry where left- and right-phenotypes differ in adaptive value; hence, we might be witnessing an ongoing evolutionary process where the phenotype is moving to a directionally asymmetric trait that might become fixed. It is difficult to predict what could account for a differential advantage of one nest phenotype over the other. One possibility is that the asymmetry does not confer an advantage *per se*, but it is the result of another trait that does, for instance brain or behavioral lateralization[1–3]. Alternatively, variation in the frequency of left- and right-sided nests may fluctuate with demographic processes, regardless of whether both phenotypes have any adaptive value. Either scenario could explain the non-random occurrence of horneros' nest asymmetry at the population level.

Environmental variables can be important drivers of bilateral asymmetries[1]. For each nest location we thus gathered data on altitude, temperature and precipitation, as these can be correlated with ecological factors such as predation pressure[7], which among others is hypothesized to influence bird nest design[8]. Through the vast geographic area covered by our study, we found no support for a relationship between the occurrence of nest asymmetry and environmental variables (Tables S1 and S2). Nest asymmetry was also not explained by nest site selection properties (Tables S1 and S2), another aspect that is proposed to influence nest architecture[8]. The occurrence of left or right nest asymmetry could be driven by unmeasured micro-climatic variables. However, this is at odds with the pattern (i.e. positive autocorrelation) that we found whereby nests with the same asymmetry are clustered spatially (beyond the territory level; Figure S1), or by the fact that territories with more nests have smaller probability of shared asymmetry (Figure 1F; $P_{(dif)} > 95\%$ comparing territories with two, three and four nests; Table S3). The latter more likely reflects changes in the territory holders (e.g. territory shift or mortality increasing with time) rather than temporal changes in micro-climatic conditions.

Although a cultural contribution cannot be totally disregarded, the occurrence of bilateral asymmetry in nest architecture could be genetically determined. The repeatability of a trait sets the upper limit to its heritability values[9]. The repeatability of nest bilateral asymmetry was $R = 0.65$ (i.e. a pair is very likely to build nests with the same asymmetry through consecutive breeding seasons; $p < 0.001$; Supplemental information), which is among the highest values reported for animal behaviors (associated to innate courtship displays) and the highest for a nest phenotypic trait[10]. The outstanding repeatability of nest bilateral asymmetry explains the higher probability of multiple nests having the same asymmetry in one territory (i.e. 'shared asymmetry'; Figure 1E) compared to a randomly generated pattern (Figure 1F; $P_{(dif)} > 99.99\%$ for model estimates vs. random simulations, Table S3; n = 544 territories). Horneros reside and breed in one territory for three consecutive years on average (with a maximum of seven years) and territories do not overlap[6]; hence, we confidently attribute the repeatability estimate to territorial pairs.

Here, we describe and quantify a bilateral asymmetry in an extended phenotype and the first one in an avian nest. The lack of support for environmental factors explaining the occurrence of nest asymmetry and the high repeatability observed at the pair level suggests that an individual, or pair, is capable of building one asymmetric phenotype only. It will be necessary to evaluate whether the 'decision' on the nest's asymmetry depends on both or one individual. Nest asymmetry could also be consequence of individual's lateralized behavior where coordination during nest building might be important. Nest asymmetry could be an assortative trait too. Follow-up observational and experimental studies will resolve such questions. The binary nature and the remarkable repeatability of asymmetric nest architecture makes it a candidate trait to seek for the genetic basis of nest building.

SUPPLEMENTAL INFORMATION

Supplemental information including one figure, three tables, a list of citizen scientists, experimental procedures and supplemental data can be found with this article online at https://doi.org/10.1016/j.cub.2022.03.075.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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Supplemental information

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Data availability statement
The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation upon acceptance.
[https://data.mendeley.com/datasets/9745v8tj9h/1; DOI:10.17632/9745v8tj9h.1]

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Conceptualization, N.M.A. and L.M.; Methodology, N.M.A. and L.M.; Analysis, N.M.A. and M.V.; Data Collection, N.M.A., L.M. and C.S.; Writing – Original Draft, N.M.A.; Writing – Review & Editing, N.M.A. and L.M.; Funding Acquisition, N.M.A. and L.M.; N.M.A. and L.M. contributed equally.

Supplemental Tables and Figures

Fixed effects β (95% CrI)		Back-transformed estimate (95 % CrI)
Intercept	0.256 (0.188; 0.323)	0.56 (0.54; 0.59)
Temperature	0.017 (-0.048; 0.084)	0.5 (0.48; 0.53)
Precipitation	0.001 (-0.067; 0.067)	0.5 (0.48; 0.53)
Altitude	-0.02 (-0.084; 0.054)	0.5 (0.47; 0.52)
Nest Height	-0.022 (-0.08; 0.037)	0.49 (0.47; 0.51)
Nest substrate	-0.027 (-0.095; 0.034)	0.49 (0.47; 0.52)
Urbanization	-0.049 (-0.113; 0.007)	0.49 (0.47; 0.51)
Nest Cover	-0.055 (-0.113; 0.012)	0.49 (0.46; 0.51)
sin(Entrance Orientation)	0.049 (-0.007; 0.100)	0.51 (0.50; 0.53)
cos(Entrance Orientation)	-0.033 (-0.088; 0.021)	0.49 (0.48; 0.51)
Autocorrelation term	**0.070 (0.005; 0.135)**	**0.52 (0.49; 0.54)**
Random factors σ2 (95% CrI)		
Observer ID	0.061 (0.054; 0.067)	

Table S1. Nest site properties and large-scale environmental condition do not explain the variation in nests' bilateral asymmetry. The response variable 'nest asymmetry' (0=Left, 1=Right) was modelled with a binomial generalized linear mix effect model. Estimates of fixed and random parameters with their 95% Credible Intervals (CrI) are shown in brackets. Statistically meaningful effects are marked in bold.

Nest asymmetry (*0=Left, 1=Right*)		
Fixed effects β (95% CrI)		*Back-transformed estimate* (95 % CrI)
Intercept	**0.250 (0.200; 0.300)**	**0.56 (0.55; 0.57)**
Temperature	-0.017 (-0.006; 0.03p)	0.5 (0.48; 0.51)
Precipitation	0.010 (-0.037; 0.056)	0.5 (0.49; 0.51)
Altitude	-0.032 (-0.077; 0.014)	0.49 (0.48; 0.50)
Nest Height	0.016 (-0.021; 0.054)	0.5 (0.49; 0.51)
Nest substrate	-0.010 (-0.055; 0.035)	0.5 (0.49; 0.51)
Nest Cover	**-0.047 (-0.092; 0.002)**	**0.49 (0.48; 0.50)**
Urbanization	-0.011 (-0.05; 0.031)	0.5 (0.49; 0.51)
Spatial Autocorrelation	**0.066 (0.006; 0.125)**	**0.52 (0.50; 0.53)**
Random factors σ^2 (95% CrI)		
Observer ID	0.048 (0.044; 0.051)	

Table S2. Environmental sources of variation of nest asymmetry in hornero's nests excluding the nest entrance orientation as a co-variate. The response variable 'nest asymmetry' was modelled with a binomial error distribution. Estimates of fixed (β) and random (σ^2) parameters with their 95% Credible Intervals (CrI) are shown in brackets. Statistically meaningful effects are those where the CrI do not overlap cero and are marked in bold.

Probability of shared asymmetry (0=*Mixed asymmetry, 1=Shared asymmetry*)			
	Fixed effects β (95% CrI)	*Back-transformed value* (95% CrI)	*Probability expected by chance* (95 % CrI)
Intercept*	1.12 (0.90; 1.33)	0.75 (0.71; 0.79)	0.25 (0.21; 0.29)
Three-nest territories	**-0.47 (-0.95; 0.007)**	0.66 (0.55; 0.74)	0.125 (0.065; 0.194)
Four-nest territories	**-1.03 (-1.89; -0.188)**	0.52 (0.32; 0.71)	0.063 (0.000; 0.174)
Five-nest territories	-0.83 (-2.34; 0.644)	0.57 (0.23; 0.85)	0.030 (0.000; 0.143)
Six-nest territories	-2.23 (-4.55; 0.09)	0.25 (0.03; 0.77)	0.015 (0.000; 0.25)
Seven-nest territories	-1.14 (-3.11; 0.83)	0.5 (0.12; 0.87)	0.008 (0.000; 0.25)

* The reference value (intercept) belongs to two-nests territories

Table S3. Probability of shared asymmetry in territories with increasing number of nests. The response variable shared asymmetry' was modelled with a binomial error distribution (*n = 544 territories*). Estimates of fixed (β) parameters with their 95% Credible Intervals (CrI) are shown in brackets. Statistically meaningful effects are those where the CrI do not overlap cero and are marked in bold. This is not the case for 'Three-nest territories' but we marked in bold because it is a remarkable effect size with a minimal overlap with zero.

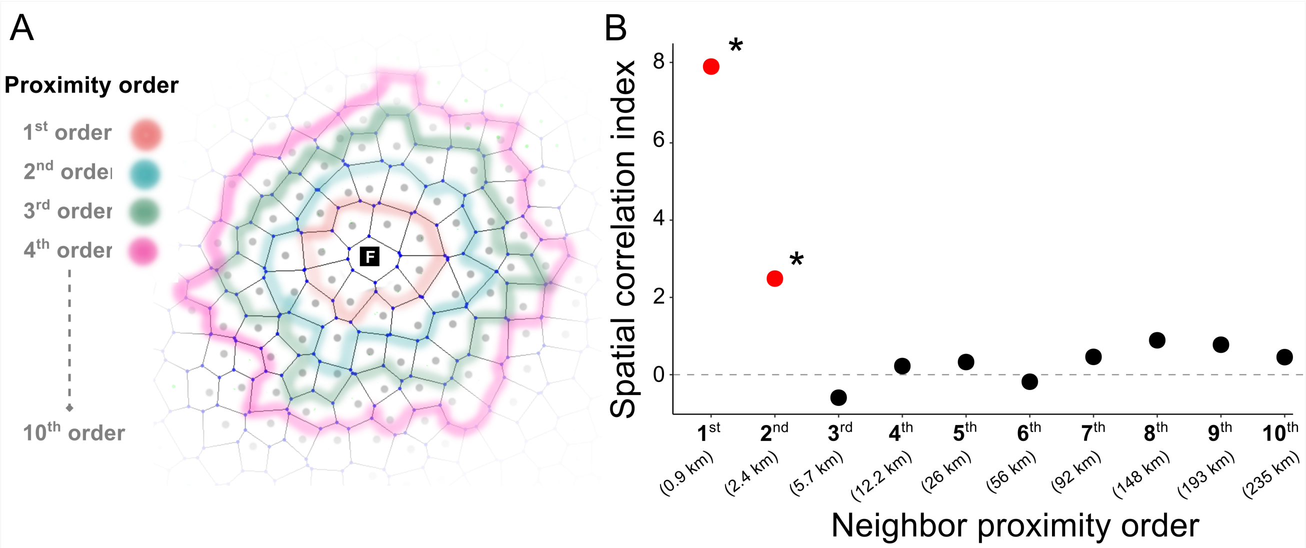

Figure S1. Neighboring nests share the type of bilateral asymmetry. (A) Dirichlet polygons approach (See STAR Methods). The spatial correlation of the asymmetric phenotype from each focal nest ('F', black square in the center) with that from its neighbors (grey dots) was calculated for different proximities (i.e., neighbors proximity order; color coded). **(B)** Spatial correlation index (Join Count Statistic) calculated for right-entrance neighbors of different proximity order (1^{st}-10^{th}). The median distance between a focal nest and its neighbors is depicted between brackets for spatial reference. Asterisks and red dots indicate the spatial correlation indexes with statistical support for a positive spatial correlation (i.e., grouped pattern of nests with the same asymmetry; 1^{st} order: $p < 0.0001$; 2^{nd}: $p = 0.03$). Running the same analysis we found comparable results, for left-entrance nests.

Supplemental experimental procedures

Data collection

Citizen-science method

We designed and released a free smartphone application available for Android and iOS devices both in Spanish and Portuguese language (i.e., the primary languages in the studied countries). To increase our reach, we advertised the project through social media platforms (@nidohorneros in Facebook, Instagram and Twitter) in Spanish, Portuguese, and English. The application was downloaded and used across the 5 countries where the rufous hornero (*Furnarius rufus*, hereafter termed 'hornero') occurs: Argentina, Uruguay, Brazil, Bolivia, and Paraguay. Horneros and their nests are cultural symbols in each of these countries (e.g., it is the national bird of Argentina) and most of the people can recognize the 'clay-oven' nest, which is distinct from the nest of every other bird species across most of its distribution. This assured us, first, that data collection would be a motivating task for the citizen scientists, and second, that nest identification by citizens would be reliable.

Data collected via HORNERO smartphone application

The smartphone application consisted of an eight steps pseudo multiple choice questionnaire that the users had to complete *in-situ* every time they encountered an hornero's nest. The questions were designed carefully so that their interpretation was unequivocal and were accompanied with guiding schemes when necessary. The different variables requested were: i) asymmetry type (whether the nest was left- or right-sided); ii) nest height (citizen scientist's height estimation of the nest between 0 and 15 m); iii) nest substrate (whether the nest was built on a natural or an artificial structure), iv) urbanization level (whether the nest was in a natural, rural or urban habitat); v) nest cover (whether the nest was covered or uncovered); vi) nest entrance cardinal orientation (the nest entrance cardinal orientation estimated by the magnetic sensor of the mobile phone); vii) nest picture; and viii) nest location (GPS coordinate automatically acquired). A detailed description of the data curation and validation process can be found in the Section 1.3.

Multiple-nest pictures data acquisition

The longevity record for the hornero so far is of 7 years[1] (Adreani & Mentesana, personal observation) and pairs have been found to reside (and breed) in the exact same territory during up to 7 consecutive years[1]. Furthermore, horneros are territorial year-round and build a new nest every breeding season[1] . Given that the nest is very resistant it is not rare that old nests persist over consecutive breeding seasons and new nests are built in the exact same location (i.e., by the side or on top of the old one; Figure 1C; Adreani & Mentesana personal observation). For these cases a picture may contain more than one nest (e.g., Figure 1C). This represents a unique opportunity to explore the repeatability of the trait at the territory level and given the life history of the birds (i.e., long-lived birds and territorial year-round) it is also valid to extend the interpretation of the results to the pair-level.

To assess the probability of shared asymmetry and to calculate the repeatability of the trait at the territory level we generated a data base with pictures that contained two or more rufous hornero nests with distinguishable asymmetry. The main source of pictures was our own database but here rufous hornero's nests from Brazil were underrepresented. Thus, for the data collection period, we also screened two additional sources of pictures: 1) the WikiAves database (https://www.wikiaves.com.br/) using the advanced search with the keywords '*Furnarius rufus'* in the species and selecting 'nests' in the photo content and 2) all the pictures from Instagram (https://www.instagram.com/) with the hashtags: #multinido; #condominio, #hornero; #joaodebarro; #rufoushornero and #furnariusrufus. Although in some cases multiple nests in the same location appeared in different pictures (i.e., presumably the same territory), we excluded these cases. We only considered the cases where all the nests (and their asymmetry) were visible in one. Thus, we assumed that each picture represented one territory. In total we found 583 nests that met these criteria: 427 from our dataset, 96 from Instagram and 60 from WikiAves. For each picture (i.e., territory) we counted the total number of nests and assigned a label of 'shared asymmetry' if all the nests had the same asymmetry and 'mixed asymmetry' if at least one nest had a different asymmetry. We only used categories with at least 4 photos (i.e., 2-7).

Statistical analyses

All the analyses were performed in R v. 3.6.1[7]. Except for the Join Count Statistics analysis, which was performed and interpreted under a frequentist framework, we performed all our analyses using the packages *'lme4*'[2] and '*arm*'[3] under a pseudo-Bayesian framework with non-informative priors. For every linear model (package "*lme4*") the restricted maximum likelihood estimation method was applied, and all the assumptions were checked *via* visual inspection of the residual plots. We used the '*sim*' function to simulate posterior distributions of the model parameters. Based on 10,000 simulations, we extracted the mean values and 95% credible intervals (CrI) of the model parameters[4]. Assessment of statistical support was obtained from the posterior distribution of each parameter[5]. We considered an effect to be statistically meaningful when the posterior probability of the mean difference (termed *p(dif)*) between compared estimates was higher than 95% or when the effect size did not overlap with zero. For details on this approach see Korner-Nievergelt et al. (2015) [5].

1.3.1 Intercept-only model to test for stochasticity of the asymmetry

To determine the population-level proportions of right and left nest asymmetry we carried out an intercept only generalized linear mixed effect model (‘*glmer*’) with a binomial distribution. Nest asymmetry (binomial, left or right) was the dependent variable and we included the citizen scientist ID as a random factor to account for the among-observer variation.

Effect of geographic and nest site environmental variables on nest asymmetry

To investigate if environmental factors could explain the variation in nest asymmetry, we ran two generalized linear mixed effect models (‘*glmer*’) with binomial distribution. Here, we only used nests for which we had GPS data (12,255 out of 12,606). We ran one model without considering the information of the nest entrance cardinal orientation and another one including this as an explanatory variable. The reason for this separation is that some devices with which photos were taken did not have the sensor that allows to determine cardinal information. Thus, for the first model we used 12,255 nests and for the second one we only used a subset of 5,557 nests corresponding to those recorded by smartphones with the corresponding sensor.

In both models the dependent variable was the binomial trait: nest asymmetry. The large-scale explanatory variables were: i) Annual mean temperature of the warmest quarter; ii) annual mean precipitation of the warmest quarter and iii) altitude (m asl). This information was extracted from Karger et al. (2017)[6]. The local-scale explanatory variables were extracted from the HORNERO App database (see section 11.1.2 for details) and consisted of i) user-estimated height of the nest (m); ii) structure where the nest was built (natural or artificial); iii) the urbanization level at the nest location (natural, rural or urban) and iv) nest cover (protected or not). Furthermore, we added a spatial covariate to account for spatial autocorrelation (see details in the last paragraph of this section). Finally, we also included 'User ID' as a random factor. All the variables included in the models were z-transformed using the function ‘scale’ from the package Base [7]. Details on the first model estimates are in Table S2.

For the second model we included the nest-entrance orientation following Pinheiro & Bates (2006)[8]. This information was recorded by the smartphone application in degrees. 0° corresponded to north, 90° corresponded to east, 180° corresponded to south and 270° to west. Given the circular properties of nest orientation data some transformation was required before its inclusion in the model[8] . First, degrees were transformed into radians. Then, each value was decomposed into its sine and cosine, corresponding to north-south and east-west contributions, respectively. Hence, the model had two explanatory variables related to the nest orientation. Details on this model are available on Table S1.

To account for spatial autocorrelation, we added a spatial covariate to our models based on Bardos et al. (2015)[9]. Specifically, we first extracted the response residuals from a non-spatial model[10] and computed the spatial auto covariation using a symmetric neighborhood matrix [9], a neighborhood distance of 10 km and an inverse squared weighting scheme. To do so we applied the function '*autocov_dist*' from the package SPDEP v.1.1-3 [11,12].

Spatial distribution of the nest asymmetry: Join Count Statistics

A join count test was used to test for spatial autocorrelation of nest asymmetry. The test was run with R package SPDEP v.1.1-3 using the function '*joincount.multi'* [11,12]. The test counts the occurrences of neighbor pairs and compares it to an expected count. Specifically, the number of observed 'right asymmetry-right asymmetry' (and left asymmetry-left asymmetry) neighbor joins are compared to an expected value, under complete spatial randomness, by a z-test statistic. Consequently, positive spatial autocorrelation occurs if the number of 'right asymmetry-right asymmetry' detections is significantly higher than what would have occurred with random spatial distribution. The spatial neighborhoods were computed based on Dirichlet polygons [13] (i.e., the space that is closer to a given nest than to any other nests). The join count statistic was first computed for close neighbors (i.e.,1st order) and then subsequently for neighbors of increasing distance (2nd order, 3rd order, and so on; Figure S1). P-values of these analyses were corrected to account for false discovery rate. We only present the results for the right-entrance nests phenotype, but the same results were obtained for left-entrance nests.

To assess the generality of the spatial autocorrelation pattern, we repeated the analyses on six quadrants that were selected from the full dataset (i.e., Cross validation). We selected the quadrants based on the number of nests and surface area. We looked on the map of observations and aimed to find quadrants of different areas that had representative amounts of nests and were evenly distributed (i.e homogeneous nest density). Furthermore, we selected quadrants that were widely distributed both latitudinally and longitudinally. The area of each quadrant and the number of nests where: 1) 10400|1980 [BA city]; 2) 3700km^2 | 839 nests [Montevideo]; 3) 3200 km^2 | 2366 nests [Hugo & Co.]; 4) 234 km^2 | 259 nests [Neuquén]; 5) 350 km^2 | 310 nests [Misiones]; and 5) 625000 km^2 | 8553 nests [Pampas].

After the cross validation we found that the only consistent pattern across quadrants was the one related to 1st order neighbors, and only in the largest quadrant (i.e.,the one with the most heterogenous density) we found a positive spatial autocorrelation with 2nd order neighbors. The discrepancy of 2nd order neighbors with the whole dataset is possibly due to the heterogenous density of nests is in our dataset. Thus, it is likely that the spatial correlation with 2nd order neighbors is an artifact consequence of this.

Nest asymmetry at the territory-level

We ran a generalized linear model (‘*glm’*) to estimate the probability of shared asymmetry across territories (i.e.,pictures) with different nest numbers. The dependent variable was binomial: 'shared asymmetry' or 'mixed asymmetry' (see section 1.2.3 for details on the definition) and the explanatory variable was the number of nests within each territory. Details on this model estimates can be found in the Table S3. In addition, we ran 10,000 simulations of our dataset assuming that left and right asymmetry were equally probable to occur in consecutive building events. Here, we calculated the probability of “shared asymmetry” (Mean and 95% CrI) for the different number of nests within a territory. Finally, we also calculated the repeatability of the nest asymmetry following Nakagawa & Schielzeth (2010)[14]. To do so, we first ran an intercept-only generalized linear mixed effect model (*'glmer'*) considering each of the nests within a territory (i.e.,picture). The dependent variable was the nest asymmetry (left or right asymmetry) and the territory (i.e.,picture ID) was set as random factor with random intercept. Then, we applied the function ‘*rptBinary’* from the package ‘*rptR’* [15] and calculated the repeatability (R) on the original scale (See[14] for details).

Curation and validation of the data set

One of the major concerns in citizen-science is the accuracy with which the data is generated [16,17]. While volunteers can perform as good as specialists (e.g., [18,19]), it is also possible that volunteers do not comply with the accuracy standards expected by the researchers (reviewed in [17]).

Prior to the design of the application, we considered five possible factors that could affect the reliability of our data due to implementing a citizen-science approach through a smartphone application. These where:

- **A.** Input of nests that did not belong to the target species.
- **B.** Input of fake data.
- **C.** Incorrect assessment of the nest characteristics.
- **D.** Repeated entries of the same nest by one user (within-user pseudo replication).
- **E.** Repeated entries of the same nest by different users (between-user pseudo replication).

To minimize possible biases from **A-C**, we proceeded as follows:

(1) During the design process, we decided to include a picture of the observed nest as a mandatory step in the application. This allowed us to perform *a posteriori* control of the data quality (see below).

(2) During data collection, we curated the incoming data on a regular basis. On average we received 34.5 nests per day. These data points were uploaded in an almost-daily basis to an online record map available in the project's homepage. We took this as an opportunity to screen newly collected data in search for errors and inconsistent data, and therefore remove such data when necessary.

(3) Once data collection was finished, we performed a data-quality validation. In order to do so, we randomly selected sets of 100 pictures from the final dataset and assigned to each figure a 'valid' or 'invalid' label. A nest was labelled as 'valid' whenever it contained a nest with a visible asymmetry, otherwise it was labelled as 'invalid'. We then calculated the proportion of valid data points over the total. We did this repeatedly, adding new sets of 100 nests until we found that the proportion of valid/invalid labels stabilized. A plateau was reached after 1000 nests. We named this final set as 'Validation subset'. Out of the 1000 pictures from this validation subset (~10% of the total number of pictures), 95,3% had a complete hornero nest with a clearly visible asymmetry. The remaining 4,7 % were composed of: 'unfinished nests' (3,1%), 'Nest in indistinguishable state' (1,3%) or 'absence of nest' (0,3%). From the 953 pictures that had a complete nest, 98,11% had correctly assigned nest properties and only 1.89% had wrongly assigned the nest asymmetry. Nest height estimation was the only nest property that we could not control from the picture. Altogether, we are confident that less than

5% of the data collected by the citizen scientists constituted a source of statistical noise in our analyses and given our final sample size, it is unlikely that this would influence our results.

To minimize and quantify possible pseudo-replication problems (points **D** and **E**) we took the following actions:

(1) Prior to the release of the application we set the duration of the data collection period to one year: from the 22nd of October of 2018 until the 31st of October of 2019 (370 days in total). Horneros are territorial year-round, breed seasonally and build a new nest every season[1,20]. Given that the nests are very resistant and that birds are territorial year-round it is not rare to find multiple nests from one pair (from current and previous seasons) in one territory[1]. By restricting the data collection period to one year we captured a 'snapshot' of the nests distribution by minimizing the collection of multiple nests from the same individuals.

(2) During data collection we encouraged the users to avoid registering the same nests multiple times weekly *via* social media platforms and developed an 'almost live' online map of observations (updated daily) that was made available in the project's homepage. We constantly brought the users attention to this resource and encouraged them to discover unexplored places and to avoid areas that were already covered by other users. In this way, we minimized between-users pseudo replication.

(3) We used the GPS information to quantify the proportion of nests in our data set that were closer than 25 m to another nest. We did pairwise distance comparisons between all nests and only 3.8% of the nests were closer than 25 m to another nest. When examining the pictures of these nests we noticed that in fact very few of these cases were duplicate records of the same nest but rather multiple different nests in the same location, which then turned out useful for other analyses (See section 1.2.3).

Except for the intercept-only model and the repeatability picture-analyses (see details above), all the nests that were registered from smartphones without an internal GPS were excluded from the analyses (351 out of 12,606 nests lacked precise GPS information).

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