








Nest traits for the world's birds

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Abstract

Motivation: A well-constructed nest is a key element of successful reproduction in most species of birds, and nest morphology varies widely across the class. Macroecological and macroevolutionary studies tend to group nest design into a small number of discrete categories, often based on taxonomic inference. In reality, however, many species display considerable intraspecific variation in their nest-building behaviour, and broad-level categories may include several functionally distinct nest types. To address this imprecision in the literature and facilitate future studies of broad-scale variation in avian parental care, we here introduce a detailed, global comparative database of nest building in birds, together with preliminary correlations between these traits and species-level environmental variables.

Main types of variables contained: We present species-level data for nest structure, location, height, material composition, sex of builder, building time and nest dimensions.

Spatial location and grain: Global. Maps are presented at the $1^0 \times 1^0$ level.

Time period and grain: Included species are generally extant, although we present some data for recently extinct taxa. The data were collected in 2017–2021 and was drawn from secondary sources published in 1992–2021.

Major taxa and level of measurement: Partial or complete trait data is presented for 8601 species of birds, representing 36 of 36 orders and 239 of 243 families.

Software format: Data have been uploaded as Supplementary Material in .csv format and are separated by species and source for all traits (Dataset S1, and Metadata) as well as summarized at the species level for the major structure and location variables (Dataset S2, and Metadata).

KEYWORDS

bird nests, nest height, nest location, nest materials, nest structure, parental care

1 | INTRODUCTION

Nest-building behaviour is widespread in birds, and variation in nesting properties is thought to reflect both lineages' evolutionary

histories (Collias, 1997; Fang et al., 2018; Medina et al., 2022; Price & Griffith, 2017) and species' adaptations to their environments (Collias & Collias, 2014; Deeming & Mainwaring, 2015; Mainwaring et al., 2014). For example, the most speciose order of

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birds, the Passeriformes (passerines), is believed to have evolved from a cavity-nesting ancestor (Collias, 1997; Fang et al., 2018), with transitions first to dome nests and then to cup-shaped nests (Fang et al., 2018; Price & Griffith, 2017); such an evolutionary history potentially represents trade-offs between the former's protection from predators and the environment (Hall et al., 2015; Martin et al., 2017; Matysioková & Remeš, 2018) and the latter's facilitation of niche exploration and modification (Collias, 1997; Fang et al., 2018; Medina et al., 2022; Odling-Smee, 2013; Price & Griffith, 2017). Interspecific variation in avian nest morphology has been linked to a range of ecologically important traits, including clutch size (Jetz et al., 2008), developmental durations (Cooney et al., 2020; Minias & Janiszewski, 2023; Street et al., 2022), brain structure (Hall et al., 2013) and correlations between body size and climate (Mainwaring & Street, 2021), while the relationship between nest morphology and egg shape (Birkhead et al., 2019; Stoddard et al., 2017, 2019) and of nest traits and environmental variation (Englert Duursma et al., 2018; Martin et al., 2017; Medina, 2019; Perez et al., 2020) remains actively debated.

Broad-scale studies of variation in nest morphology and location, however, often aggregate many different nesting behaviours into a few, broad categories. For example, Stoddard et al. (2017) scored nest location as 'non-cavity ground', 'non-cavity elevated' or 'cavity' and nest structure as 'scrape/bed', 'plate' or 'cup', neglecting, for instance, the potential impact of domed nests. Other sources conflate structure and location: Jetz et al. (2008), for example, coded nest type as 'open', 'half-open' or 'closed', while Cooney et al. (2020) coded nest type as 'cavity', 'closed', 'open' or 'mixed'. Such groupings can obscure the varying ecological costs and benefits of different strategies (Vanadzina, Street, & Sheard, 2023). For example, while enclosed nests are thought to be associated with increased protection from predators (Lack, 1948), obligate cavity nesters face much stronger competition for nest sites than do facultative cavity nesters (Martin, 1993a; Martin & Li, 1992). An exhaustive species-level coding system that carefully distinguishes among many different nest morphologies and strategies would allow researchers to both examine questions in greater detail than has hitherto been possible and to easily construct their own categorizations that are tailored to specific scientific questions.

Furthermore, nest structure and location are often assumed to be invariant at higher taxonomic levels. For example, Jetz et al. (2008) inferred 'nest type' within genera, whereas Price and Griffith (2017) and Fang et al. (2018) scored nest shape/structure, location and exposure/placement at the family level. While this strategy is appropriate for some types of questions, taxonomic inference ignores the tremendous intraspecific and intra-taxon variation in nest behaviour that can be found in the world's birds (Billerman et al., 2022; Collias & Collias, 2014; Hansell, 2000; Perez et al., 2023), as well as the many gaps English-language Western science has in its knowledge of biodiversity, particularly tropical natural history (e.g., Lees et al., 2020).

Here, we present a detailed database of nest traits (structure, location, height, materials, sex of builder, building time and size) for the world's birds (Figure 1). We record intraspecific variation where appropriate, and we note both uncertainty in our coding and where we were unable to find species-level information. We also present a phylogenetically corrected summary of major environmental and morphological correlates of key global variation in nest structure and location, as well as an exploration of geographic biases present in our dataset. We hope that this level of precision and broad taxonomic scope will facilitate future studies of the macroecology and macroevolution of avian parental care as well as direct attention to fruitful directions for future research.

2 | DATA COLLECTION

We targeted text descriptions and photographs published in three sources of information: the Handbook of the Birds of the World Alive (2017–2018), Neotropical Birds Online (2019–2020) and the Birds of North America Online (2019–2021), using the BirdLife International taxonomy. Note that these three sources have subsequently been combined into a single resource, the Birds of the World (Billerman et al., 2022), under a different taxonomy, the eBird/Clements checklist. Coding was done by six researchers (CS, SES, CAT, ADC, AY and AT). Two sets of researchers (CS, CAT and ADC; CS and AY) were able to meet regularly to mutually resolve any uncertainties to agreement; most of the data collected by the other two researchers (SES and AT) were checked and, if necessary, re-coded by a second coder (CS). Two researchers (CS and SES) also each spot-checked an arbitrary set of species. In total, 4072 entries (25.5%) were checked by at least one person other than the original coder. We include coder and checker identity in our published database, however, in recognition that observer bias potentially remains.

This data collection process at times generates instances of uncertainty, such as due to vague textual descriptions, unclear photos or information reported in the secondary source as being suspicious to the author of that source. For example, an entry might note that a species nests in a cavity, but it may not be clear whether that species excavates that cavity or not. We therefore introduced a measure of *uncertainty* in our coding scheme, which allowed the coder to mark for the possible presence of a trait. These uncertainty scores not only indicate potential avenues for future research but could also be retained as data within comparative analyses, either in sensitivity analyses or within packages that permit uncertain trait values, such as BayesTraits (Pagel et al., 2004) or Claddis (Lloyd, 2016).

We included only breeding nests (i.e., the location of the eggs), rather than any other nest-like construction (e.g., display courts, roosting sites). Our fine-grained classification approach also targets, where possible, the builder's own actions, allowing researchers to distinguish structures constructed by the focal

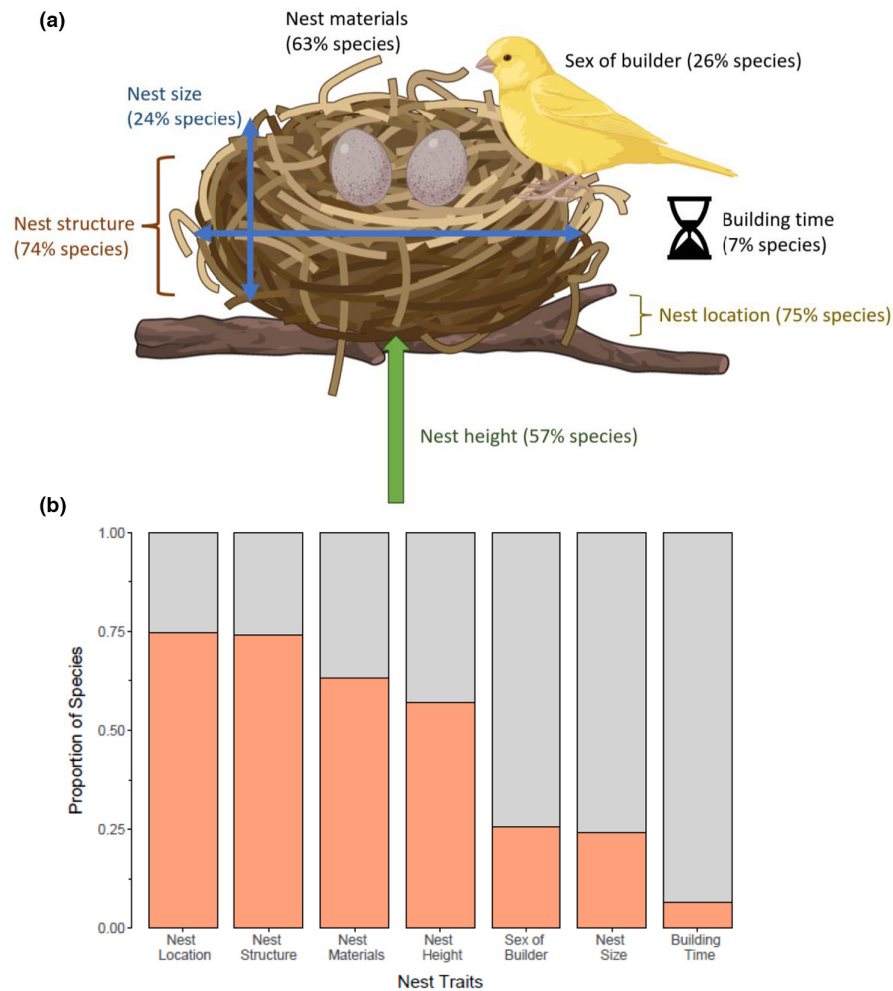


FIGURE 1 Nest traits contained within this dataset. (a) Graphical display of nest traits and (b). proportion of data completeness, based on the 11,121 species listed in the 2017 Handbook of the Birds of the World Alive and includes some extinct species. Icons of the bird, nest, eggs, and tree branch were obtained from BioRender and are intended as illustrative and not to indicate ornithological accuracy.

species versus pre-existing structures adopted by that species. Further information on each of these variables can be found in the Supplementary Materials.

2.1 | Nest structure

Inter-specific variation in nest structure is thought to correlate with differences in protection from predators and the environment (Collias, 1997; Englert Duursma et al., 2018; Mainwaring et al., 2014; Martin et al., 2017; Medina, 2019), as well as facilitate or limit the exploration of new ecological niches (Medina et al., 2022; Odling-Smee, 2013). We here distinguish among nine major types of constructed nest structures (Figure 2): *none* (birds that lay their eggs directly onto bare substrate or into pre-existing, unmodified cavities; e.g. Keel-billed Toucan, *Ramphastos sulfuratus*), *scrape* (an open, shallow depression created by the bird, with or without a lining; e.g. Dunn's Lark, *Eremalauda dunnii*), *platform* (a shallow, flat or saucer-shaped nest with a constructed base and a central depression; e.g. Horned Screamer, *Anhima cornuta*), *cup* (a constructed nest with walls and a base; e.g. Andean Hillstar, *Oreotrochilus estella*), *dome* (an enclosed, roofed nest with a small entrance hole; e.g. Dusky Antbird, *Cercomacroides tyrannina*),

dome-and-tube (a multi-chambered dome, such as a dome plus an internal or external entrance hole, including large communal structures; e.g. Yellow-mantled Weaver, *Ploceus tricolor*), *excavation* (an enclosed cavity created by the species itself; e.g. Rainbow Bee-eater, *Merops ornatus*), *cavity modifier* (an enclosed cavity formed by a pre-existing cavity subsequently modified by the species itself; e.g. Thick-billed Parrot, *Rhynchopsitta pachyrhyncha*) and *excavator-with-nest* (a species that fully or partially excavates a cavity and then constructs a structure inside; e.g. Moustached Turca, *Pteroptochos megapodius*).

We also present a coding system for four rare types of nest structures: *clearing* (a location cleared of debris but with no depression created), *ring* (a location ringed with material with no depression created), *mound* (a strategy whereby eggs are buried in a mound of material, commonly associated with megapodes) and *purse* (a long, pendant pouch, likely providing protection similar to that of a dome but lacking a fully enclosed roof, found in the Icteridae). We note that, in practice, clearings and rings are considered by many researchers to be types of scrapes. For the purpose of Dataset S2, 'purse' is coded as an uncertain state between a cup and a dome.

Criteria are largely based on Hansell (2000), and full definitions can be found in the Supplementary Material. We present information

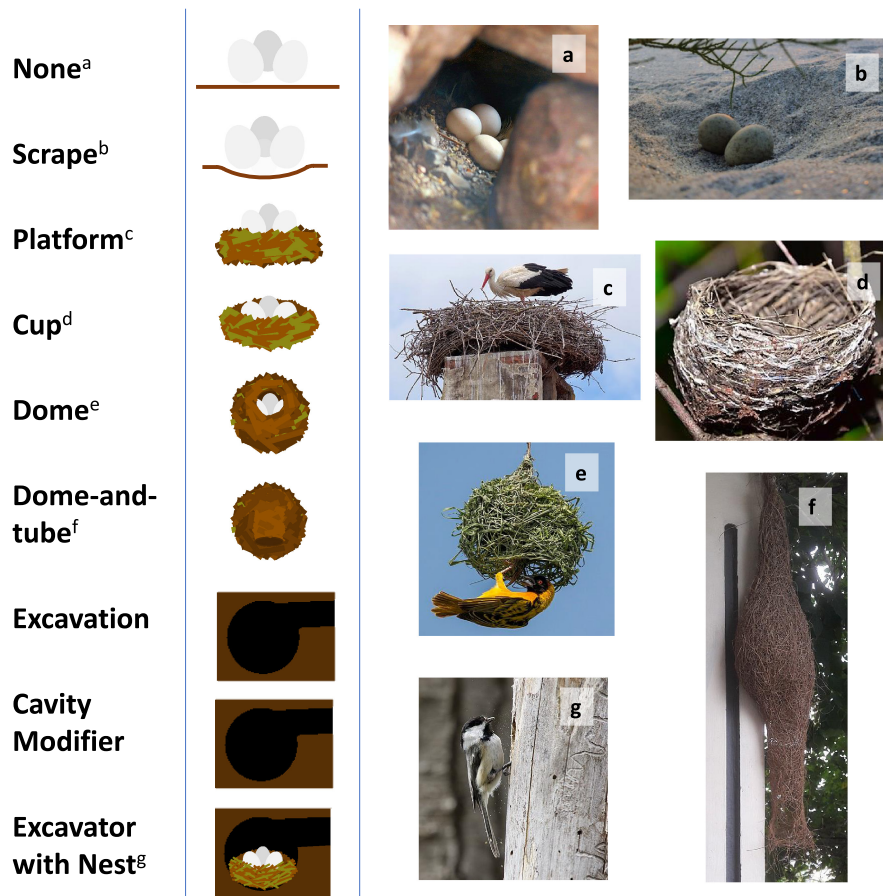


FIGURE 2 Major nest structures. Shown are graphical sketches of the seven major nest structures, along with exemplar photographs. (a) Budgerigar (*Melopsittacus undulatus*) eggs on lining but no built nest within a natural, unmodified cavity (“none”). Photo by Wikimedia user BeanieAll, CC BY-SA 4.0. (b) An example of a “scrape” nest. Photo by Aditya Pal, CC BY-SA 4.0. (c) A White Stork (*Ciconia ciconia*) “platform” nest. Photo by Jakub Hałun, CC BY-SA 4.0. (d) A Red-vented Bulbul (*Pycnonotus cafer*) “cup” nest. Photo by Wikimedia user Himalamarasinghe, CC BY-SA 4.0. (e) A Village Weaver (*Ploceus cucullatus*) “dome” nest. Photo by Charles J. Sharp, CC BY-SA 4.0. (f) A “dome-and-tube” nest. Photo by A. Shaarathy, CC BY 3.0. (g) A Black-capped Chickadee (*Poecile atricapillus*) outside of a self-excavated primary or modified secondary cavity nest, in which a cup nest will typically be built (“excavator with nest”). Photo by Wikimedia user Jshamgochian, CC BY-SA 4.0. All photographs were stylistically modified. Nest structure graphical illustrations by Sally E. Street, based on fig. 1 of Vanadzina, Street, & Sheard, 2023. [Correction added on 1 December 2023, after first online publication: Figure 2 has been updated in this version.]

on nest structure for 8227 species (9569 entries), including our uncertainty metric.

2.2 | Nest location

Nest location has been found to correlate with clutch size (Jetz et al., 2008) and potentially with egg morphology (e.g., Birkhead et al., 2019, though see Stoddard et al., 2017, 2019), as well as to co-evolve with nest structure (Fang et al., 2018; Hall et al., 2015). We here distinguish between seven major categories of nest locations (Figure 3): *artificial structures* (e.g., fences, roofs, nest boxes), *earthen holes*, *ground*, *elevated rocks*, *tree holes*, *elevated vegetation* (including a subclassification separating out attachments to bushes, trees and reeds) and partially submerged in *water*. Criteria are largely based on Hansell (2000), and full definitions can be found in the Supplementary Material. We present information on nest locations for 8305 species (9699 entries).

2.3 | Nest height

Nest height is often used as a proxy for predation, with higher nests thought to be less accessible to predators (Lima, 2009; Martin, 1993b; Matysioková & Remeš, 2023). We here present values for the minimum and maximum nest height in metres, where available, and note that ground nests are sometimes slightly elevated by, e.g., grass tussocks. We present information on nest height for 6330 species (7315 entries).

2.4 | Nest materials

The materials used to construct a nest can reflect various physical and mechanical properties, including those known or thought to contribute to offspring survival (Bailey et al., 2014; Bailey et al., 2016; Biddle et al., 2018; Breen et al., 2021; Hilton et al., 2004). We here

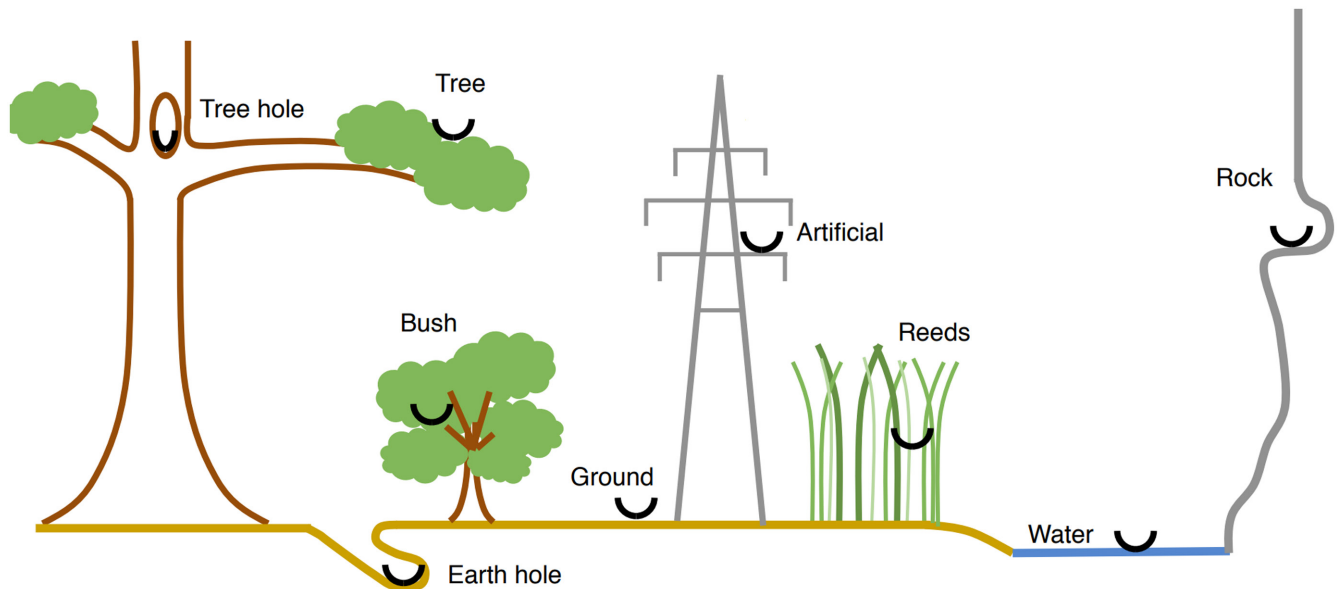


FIGURE 3 Major nest locations. Shown are the seven major nest locations, including the three sub-types of vegetation (tree, bush, and reeds). See below for definitions. Drawings by Sally E. Street.

present a compilation of recorded nest materials as listed in the three consulted sources, which researchers can then search for or score for various properties of interest. These lists are likely to vary substantially with spatial scale and research effort (Jagiello et al., 2023; Sheard, Stott, et al., 2023). We present information on nest materials for 7020 species (8192 entries); for one potential categorization of these materials, see Sheard, Street, et al. (2023).

2.5 | Sex of builder

Sex-specific contributions to nest building vary by species as well as with the stage of the nest building process (e.g., site selection, material gathering, material weaving, nest lining; Mainwaring et al., 2021; Soler et al., 1998). There is substantial in-specific variation in the sex-specific contributions to these various stages, and different aspects of this process may be of interest to different researchers. To maximally preserve potentially relevant information, we thus here include raw species-level descriptions rather than an overall classification. We present information on sex-specific building activities for 2839 species (3213 entries).

2.6 | Building time

The amount of time necessary to build a nest was rarely reported; for what information we could gather, however, we present the minimum, maximum and average number of days a species has been recorded as spending building a nest as a potential measure of parental investment (Medina et al., 2022). We present building time data for 723 species (794 entries).

2.7 | Nest size

We found very little regularity in the reporting of nest size; other researchers, however, may still find these dimensions useful measures of parental investment. For more information on the global correlates of size of passerine cup nests, including comparisons between textual descriptions and measurements of museum specimens as well as an analysis of inter-specific versus intra-specific variation in size, see Vanadzina, Street, Healy, et al. (2023) or Perez et al. (2023). We here present size data for 2699 species (3022 entries).

3 | DATA PATTERNS

To showcase an example use of these data, we displayed spatial variation in six key nest categories (platform, cup and dome nest structures; ground, vegetation and artificial nest locations; the first five were selected as the most common structure/locations and the sixth, artificial, due to its potential conservation interest) at the $1^{\circ} \times 1^{\circ}$ scale using the 2018 BirdLife International breeding and residential range maps (BirdLifeInternational, 2018). The distribution of platform nests was relatively uniform, although highest in the Caribbean (Figure S1a). Cup nests were most commonly found in North America and rarely found in Africa (Figure S1c); by contrast, dome nests were generally concentrated in Africa, Australia and Southeast Asia and rare elsewhere (Figure S1e). Nesting in artificial locations was strongly biased towards the Northern Hemisphere, especially in major deserts (Figure S1b). Ground-nesting strategies showed a remarkable latitudinal gradient, with increased prevalence towards the poles (Figure S1d; cf. Minias & Janiszewski, 2023, who explored this pattern within

passerines). Finally, nests attached to vegetation were common throughout the world, except at the highest latitudes and on the Tibetan plateau (Figure S1f).

To illustrate exploratory correlations between some nest structure and location traits and key environmental variables, we ran Bayesian phylogenetic logistic regressions in the R package *MCMCglmm* (Hadfield, 2010). We first reconciled inter-source variation in nest scores to produce a single species-level set of structure and location scores; for further details on this process, see the Supplementary Materials. We then obtained species-level values for average breeding range latitude, temperature, precipitation and annual variability in temperature and precipitation (i.e., temperature and precipitation 'seasonality'), as well as a species-level, sex-averaged body mass measure (Dunning, 2007) and an estimate of flight ability known as the hand-wing index (HWI; the ratio of Kipp's distance to the total wing chord) from Sheard et al. (2020). We included body mass in our models due to the well-established relationship between this variable and avian life history syndromes; we included HWI as it is an increasingly popular proxy for dispersal ability (Claramunt et al., 2012; Kennedy et al., 2016; Pigot et al., 2018; Weeks & Claramunt, 2014) and reflects a key macroevolutionary axis in avian biology, linking, for example, migratory behaviour, the defence of ecological territories and diet (Sheard et al., 2020; Weeks et al., 2022).

Models were constructed separately for each of seven most common nest structure categories (scrape, excavation, platform, cup, dome, dome-and-tube and none) and seven most common nest location categories (artificial, earth holes, ground, elevated rocks, tree holes, elevated vegetation and water; see Figure S4) as binary response variables (excluding species with uncertain scores) and were run across 100 trees randomly chosen from the Hackett backbone of the Jetz et al.'s (2012) Global Bird Tree. After an initial dummy run to determine start points, each model was run across each tree for a total of 20,000 iterations (burn-in 10,000; sampling rate 1000; for a posterior sample of 10 per tree). Priors for the fixed effects were set using the command 'gelman. prior'; priors for the phylogenetic variance were set to $V=10^{-10}$ and $\nu=-1$, and the residual variance was fixed to 1. To improve output interpretability, all continuous variables were scaled to have a mean of 0 and a variance of 1; body mass and HWI were additionally log-transformed. Further information on model specifications can be found in the published code.

Some, though not all, nest structures could be linked with the environment typical of the species breeding range: species were more likely to build cups if they lived in areas with higher precipitation, higher temperature seasonality and/or lower precipitation seasonality; more likely to build platforms if they lived in areas with higher precipitation seasonality; and less likely to build scrapes if they lived in wetter areas. Furthermore, smaller species were more likely to build domes and more likely to excavate, while larger species were more likely to build platforms or scrapes (Figure 4a). The wing morphology variable HWI was also linked to nest structure; after correcting for mass and environmental correlates, species with high

HWI (a proxy for stronger long-distance flight ability) were more likely to build cups and scrapes or entirely forgo a nest and less likely to build domes or dome-and-tube structures (Figure 4c).

Nest location was generally more closely tied to environmental variation than was nest structure. Species were more likely to nest in artificial locations in warmer and/or drier places with greater temperature seasonality and less precipitation seasonality. Species were more likely to nest in earth holes in cooler and/or drier places, and in tree holes at higher latitudes, in warmer places, in wetter places and/or in places with greater temperature seasonality. Species were more likely to nest on the ground in cooler locations, and in or near water at lower latitudes and/or in places with greater temperature seasonality. Species were more likely to nest on elevated rocks in cooler, drier and less seasonal (both temperature and precipitation) places. Species were more likely to nest in vegetation in warmer and/or rainier places with greater temperature seasonality and/or less precipitation seasonality.

Additionally, both heavier species and species with greater HWI (higher flight ability) were more likely to nest in artificial locations or on elevated rocks, while both lighter species and species with smaller HWI (lower flight ability) were more likely to nest in vegetation (Figure 4, panels b and d).

Finally, to explore potential research biases in the nest dataset by geography, we compared the proportion of species lacking nest information across biogeographical realms. We anticipated that species from tropical regions would be most likely to be underrepresented in the nest dataset, due in part to pervasive inequalities in the global distribution of research funding (e.g., Lees et al., 2020). Further details on realm scoring and data analysis can be found in the Supplementary Materials. As anticipated, we found that biogeographical realms containing tropical regions generally have more species with missing nest information compared with polar and temperate regions, with species from Oceanian and Neotropical regions particularly underrepresented (Figures S3-S6). This is especially notable in the case of builder identity, where the Nearctic realm (i.e., most of North America, plus Greenland) is the only region where >50% of species have documented data.

4 | CONCLUSIONS

We here present a species-level dataset of key nest-building traits for a large sample of birds. Our coding system improves on previous attempts with its level of detail, ability to describe intraspecific variation and lack of taxonomic inference. We have also described basic environmental and morphological correlations between major structure and location categories, demonstrating that the placement of the nest is more closely linked to broad-scale environmental variation than is the structure of the nest itself. One possible interpretation of this is that environmental factors may have driven finer scaled variation in nest features other than gross morphological type (Medina, 2019; Ocampo et al., 2023), such as nest dimensions (Perez et al., 2023; Vanadzina, Street, Healy, et al., 2023);

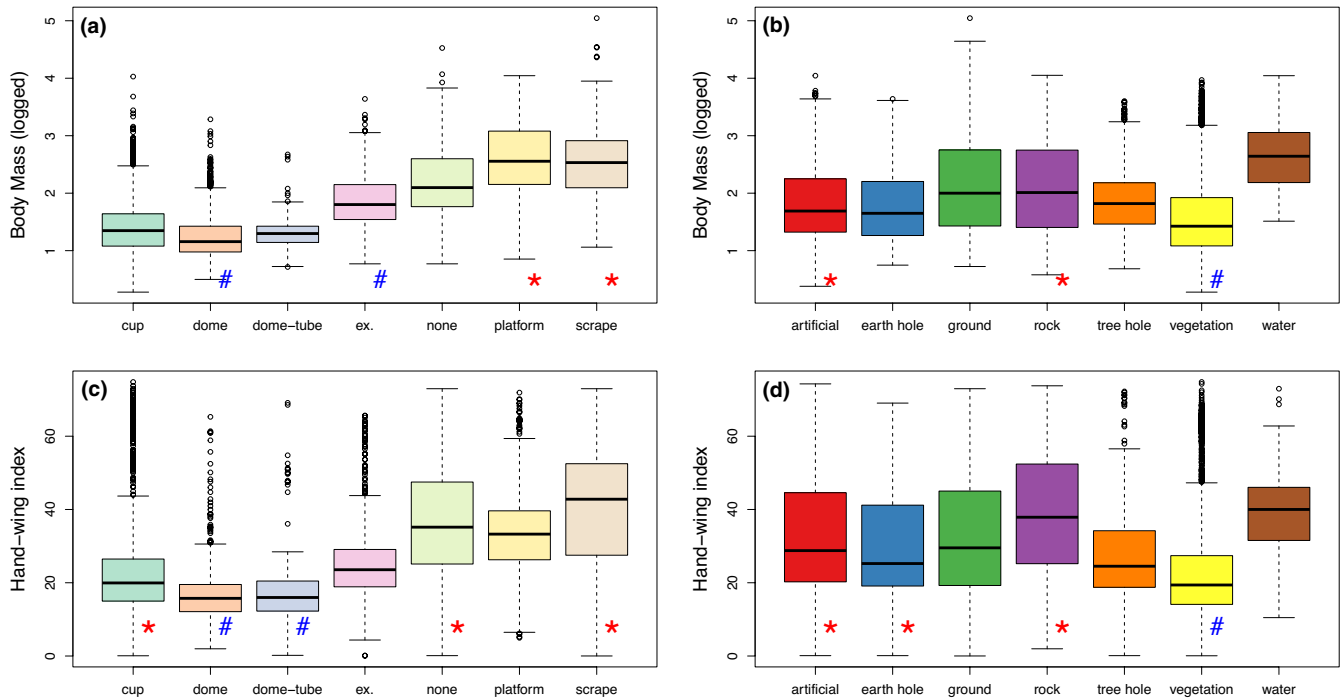


FIGURE 4 Distribution of body masses (above) and hand-wing indices (HWI, below) for nest structure (left) and nest location (right). Note that some species fall into multiple nest structure/location categories due to intraspecific variation. After correcting for the effects of covariates and phylogenetic signal, there are significant effects of body mass on the probability that species build dome, excavation, platform, and scrape nest structures (panel a), as well as nest in artificial, rock, and vegetation locations (panel b), whereas the HWI differences are statistically significant for cup, dome, dome-and-tube, none, and scrape nest structures (panel c), as well as for artificial, earth hole, rock, and vegetation locations (panel d). Positive statistically significant results are marked with a red asterisk (*) and negative statistically significant results are marked with a blue hash (#). See Tables S1–S7 for full results of the nest structure phylogenetic logistic regressions (panels a, c) and Tables S8–S14 for the nest location phylogenetic logistic regressions (panels b, d). The abbreviations “ex.” = excavations and “dome-tube” = dome-and-tube nests.

another explanation may be that nest structure is more closely linked to ecological and life history factors not considered here, such as clutch size (Heenan & Seymour, 2011) or predation rates (Collias & Collias, 2014; Hall et al., 2015; Mainwaring et al., 2015; Martin, 1993b; Matysioková & Remeš, 2022). There are also potentially differences in the level of genetic control governing species- and population-level variation in nest structure versus nest location (Fang et al., 2018; Healy et al., 2023), underscoring the importance of uniting comparative work with research into the behavioural and mechanistic basis of nest building.

There are many species about whose nesting strategies Western, English-speaking science knows nothing, particularly in the tropics (Hortal et al., 2015; Lees et al., 2020) (see also Figures S3–S6). We hope, however, that by documenting the variability in nests among well-studied species and highlighting the gaps in our knowledge, we not only provide a useful dataset for future macroecological and macroevolutionary work but also motivate future fieldwork and natural history documentation of the diverse reproductive biology and behaviour of the world's birds.

AUTHOR CONTRIBUTIONS

Sally E. Street, Catherine Sheard, Kevin N. Lala, Susan D. Healy, Karina Vanadzina and Andrew D. Clark designed the data collection

protocols. Catherine Sheard, Sally E. Street, Camille A. Troisi, Andrew D. Clark, Andrew D. Clark, Antonia Yovcheva and Alexis Trébaol collected the initial data. Catherine Sheard, Sally E. Street checked, cleaned and analysed the data. Catherine Sheard wrote the manuscript, and Sally E. Street, Karina Vanadzina, Susan D. Healy and Kevin N. Lala provided additional writing and editing. All authors approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Datasets S1 (all data) and S2 (species-level scores for nest structure and location) are included here together with their metadata as Supplementary Material and are also available at doi.org/10.5281/zenodo.10009756.

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BIOSKETCH

The author team consists of evolutionary biologists, behavioural ecologists and palaeontologists, with a shared, interdisciplinary interest in the macro- and micro-evolution of parental care.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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