

## Research



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# Nest architecture influences host use by avian brood parasites and is shaped by coevolutionary dynamics

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Brood (social) parasites and their hosts exhibit a wide range of adaptations and counter-adaptations as part of their ongoing coevolutionary arms races. Obligate avian brood parasites are expected to use potential host species with more easily accessible nests, while potential hosts are expected to evade parasitism by building more concealed nests that are difficult for parasites to enter and in which to lay eggs. We used phylogenetically informed comparative analyses, a global database of the world's brood parasites, their host species, and the design of avian host and non-host nests (approx. 6200 bird species) to examine first, whether parasites preferentially target host species that build open nests and, second, whether host species that build enclosed nests are more likely to be targeted by specialist parasites. We found that species building more accessible nests are more likely to serve as hosts, while host species with some of the more inaccessible nests are targeted by more specialist brood parasites. Furthermore, evolutionary-transition analyses demonstrate that host species building enclosed nests frequently evolve to become non-hosts. We conclude that nest architecture and the accessibility of nests for parasitism represent a critical stage of the ongoing coevolutionary arms race between avian brood parasites and their hosts.

## 1. Introduction

Interspecific brood (or social) parasitism, whereby parasitic species lay their eggs in the nests of host species, which then raise their offspring at an individual cost, has fascinated biologists since the fourth century BC, when Aristotle wondered if common cuckoos (*Cuculus canorus*) do not raise their own young [1]. Obligate vertebrate brood parasite birds are spread across five families and seven independent lineages; there are more than one hundred of such species, or approximately 1% of all avian diversity, and these are known to use more than 1700 hosts, or approximately 17% of all bird species [2–4]. Interspecific brood parasitism typically lowers the breeding success of hosts [5] (but see [6]), and thus many brood parasites and their hosts have become involved in a coevolutionary arms race: brood parasites manipulate their hosts to accept and raise the parasitic offspring, while the hosts accrue increasingly sophisticated recognition mechanisms to detect and reject the foreign propagules in their nests [7–10].

Avian brood parasites exhibit a range of adaptations for targeting hosts [7]. For example, egg-laying parasitic females attempt to be inconspicuous by watching host nests from a distance before rapidly laying their own eggs [11]. Even if they are seen, some female cuckoo parasites have predatory hawk-like phenotypes which dissuades hosts from attacking them [12,13]. Meanwhile, many specialist parasites' eggs closely mimic those of hosts to avoid detection and rejection [8,14–16] and/or have stronger eggshells to dampen pierce-rejection rates by the potential hosts [17,18], even if increased parasitic eggshell thickness is also thought to protect it from breaking during the parasite's egg laying process [19]. Some brood parasites depredate nests containing only host nestlings so that the parents are forced to re-nest with the new clutch potentially becoming available for parasitism, known as farming behaviour by the parasitic adult [20,21]. Finally, the begging calls of the offspring in several parasitic lineages mimic or even exaggerate those of host young, thus encouraging host parents to feed them preferentially over their own offspring [22,23], while the offspring of selected parasite species display gape-coloured skin patches on their wings to increase food delivery rates by their hosts [24].

Specialist brood parasites target one-to-few host species, with many having evolved highly specialized adaptations for their focal host(s), while generalist brood parasites, such as brown-headed cowbirds (*Molothrus ater*), may show competitive nestling adaptations to outcompete hosts and succeed in nests of more than 100 species [3,25]. Furthermore, generalist brood parasites can employ a 'Jack of all trades' approach to egg mimicry and lay generic eggs that have a moderate similarity to a wide range of hosts' eggs [14,26]. Accordingly, Horsfield's bronze-cuckoos (*Chalcites basalis*) lay eggs that have eggshell colours that are moderate mimic of 17 of their 27 hosts [14]. Meanwhile, shiny cowbird (*Molothrus bonariensis*) offspring adaptively alter their begging behaviours in relation to the species-specific begging behaviours of their host species [27]. Generalist brood parasites thereby exhibit adaptations that are focused on successfully parasitizing a wide range of host species [3,9].

Hosts exhibit a range of counter-adaptations to minimize the costs of being parasitized. Those defences consist of diverse behavioural, morphological, and physiological traits that are classified as being either front-line defences, egg-stage defences, or nestling- and fledgling-stage defences [28]. Front-line defences minimize the probability of parasites laying eggs in the host's nest. Hosts may do this by selecting concealed nest sites [29,30] away from perches used by parasites [31,32] or by nesting near other potential hosts to promote antiparasitic group defence [33,34]. Meanwhile, hosts can also minimize the risk of parasitism by building domed nests with narrow holes or tubes to prevent the typically larger parasites from accessing nests [35], although the use of concealed nest sites has likely evolved in response to predation [36] and/or adverse weather conditions [36].

If parasites approach nests, then hosts may mob or attack them [37]. Egg-stage defences are those that seek to minimize the chances of the parasite's egg hatching, such as the eviction of eggs that do not resemble their own [8,38,39]. In these cases, hosts have evolved to lay clutches of eggs with less variation in their appearance than the clutches of non-hosts to aid the identification of the discordant foreign eggs [40,41]. Nestling- and fledgling-stage defences, meanwhile, refer to behaviours that minimize the fitness consequences of successfully hatched parasitic offspring and relate to the discrimination, eviction, or

abandonment of non-mimetic parasitic offspring [42–45]. These host defences vary adaptively in response to the localized threat of being parasitized, with greater costs being matched by greater defences [6,10,25,46].

The coevolutionary dynamics of brood parasites and their host species are also influenced by the number of host species that are targeted by brood-parasitic species [25,47], which value ranges from specialists such as yellow-throated cuckoos (*Chrysococcyx flavicularis*) that target one host species, through to generalists like brown-headed cowbirds that parasitize hundreds of host species. Hosts targeted by specialist brood parasites are predicted to have coevolved with their parasites to accrue greater host defences [48]; for example, they are more likely to build or usurp enclosed nests [2] and/or to reject even mimetic parasite eggs from nests [49]. By contrast, the shiny cowbird, a generalist brood parasite, targeted open and closed nesting species at approximately equal rates [50]. However, most of the more than 200 known host species of these cowbirds are open cup nesting species, suggesting that even this parasitic species targets hosts with relatively exposed nests, and furthermore highlighting the need for a comparative analysis of most brood parasitic species and the nesting diversity of their hosts (and non-hosts) [50].

It has been suggested that dome and cavity nest use are adaptations against brood parasitism as they provide a physical barrier to the female parasite [7,25,35]. Indeed, a recent study showed that host species building domed nests are targeted by more specialized brood parasites [2], but this work did not examine the full phylogenetic diversity of both hosts and non-hosts and their nesting ecologies beyond a dichotomous open/enclosed nest category. Thus, our understanding of the potentially dynamic role of nest architecture in influencing host–parasite coevolution remains limited, especially regarding the generality of such processes across geographical and phylogenetic contexts [2]. Our focal hypothesis [34,35,51] is that hosts of avian brood parasites may build enclosed nests, and domed nests with long entrance tubes, as a front-line defence against brood parasites.

In our study, we examine the role of nest architecture within explicit coevolutionary arms race scenarios between brood parasites and their hosts. We used phylogenetically informed comparative analyses and a global database of the world's brood parasites and each of their host species' nest structures (1) to examine whether serving as a host species is more likely in species that have open, and thus accessible nests (as they are more easily accessible for parasitism than enclosed nests) and (2) to confirm, using a larger and independent nest architecture dataset, that host species that build more enclosed nests are targeted by specialist parasites relative to species that build less accessible nests [2] (as the specialist hosts may be more likely to have coevolved structural nest defences against specialist brood parasites). Finally, we performed (3) evolutionary-transition analyses of parasitic usage of different types of host nest structures to examine the coevolutionary dynamics of nest status and host status over evolutionary timescales.

## 2. Methods

### (a) Quantifying avian nest architecture

Avian nests were classified into five categories based on their accessibility to brood parasites: scrape nests (the most easily accessible), cup nests, domed nests, dome with tube nests and hole nests,

which included all tree and earth cavity nests. For the remaining species that do not nest in holes, we designated their nests as 'scrape', 'cup', 'dome' or 'dome with tube' nests as follows. Scrape nests consisted of those species that lay eggs in nests containing either no or minimal nest material, and thereby include those that make no discernible modification to the nest site such as tawny-throated dotterels (*Oreopholus ruficollis*) and least nighthawks (*Chordeiles pusillus*). Scrape nests should, in theory, be easily accessible to brood parasites. Meanwhile, cup nests are those nests classified as being either a cup or a platform built by, for example, passerines such as American robins (*Turdus migratorius*) and waterbirds such as mute swans (*Cygnus olor*). These nests are somewhat less accessible to brood parasitism than scrape nests because they have a defined, constructed bottom and sides and are often surrounded by thick layers of substantial vegetation cover. Dome nests are enclosed single-chamber roofed nests built by, for example, long-tailed tits (*Aegithalos caudatus*) and village weavers (*Ploceus cucullatus*) and are relatively inaccessible to brood parasites. Finally, dome with tube nests are enclosed roofed nests with distinctive entrance tubes or multiple chambers built by, for example, baya weavers (*Ploceus philippinus*), representing an even less accessible nest type for brood parasitism [35].

All species that build a single nest design ( $n = 5246$ ) were assigned to the appropriate nest classification; a further 910 species built multiple nest types and were assigned to each classification, e.g. a species that is known to build both a scrape and a cup nest was considered to build both. Therefore, we had five dummy-coded variables, where 1 indicates that a certain nest type is typical for a species and 0 denotes the opposite: 1141 scrape, 3631 cup, 1313 dome, 133 dome with tube, 929 hole. All nest data were collected from written descriptions and published photographs in the Handbook of the Birds of the World Alive (2017–2018), Neotropical Birds Online (2019–2020) and the Birds of North America Online (2019–2020), which have since been combined into the Birds of the World [52].

## (b) Identifying the world's brood parasites and host species richness

We identified the world's obligate avian brood parasites and their host species from the table provided in electronic supplementary material, data 2 [2]. The database is the result of an exhaustive search of the published literature for brood parasites and their hosts, with detailed information on that process provided [2]. Briefly, we used data on the 84 species of obligate brood parasites that were identified by Antonson *et al.* [2] and those parasites come from 19 genera and five families across seven independent origins of brood parasitism. The species included in our study therefore represent approximately 86% of all known brood parasite species, with the other 14% not included because we have insufficient respective data available about their parasitic behaviours and host uses. The database also contains data on the known host species ( $n = 1398$  of which overlap with our nest dataset; see above) that are targeted by each of these brood parasites. We surveyed the number of different host species used by each parasite targeting each host taxa, and took the lowest of these host-species richness values: thus, for each host species this approach provides a numerical value for their parasites' maximal extent host specialization. Finally, all those bird species not listed as hosts or parasites in the table provided in electronic supplementary material, data 2 [2] were therefore defined as non-hosts ( $n = 4809$ ) in our larger dataset of avian species' nests (see above).

## (c) Statistical analyses

We built two major models to explain variation in nest architecture in potential host species. The first model contained host status as the response variable and the five nest architecture

categories as predictors. The second model, meanwhile, included only parasitized hosts and had their respective species of parasites' lowest host-species richness (a measure of host-specific parasite specialization) as the response variable with the five nest architecture categories as predictors.

We applied a Bayesian framework to fit our models. We first fitted generalized linear mixed models using Markov chain Monte Carlo techniques ('MCMCglmm' package [53]) to enable us to control for the phylogenetic relationships of species by including the inverse relatedness matrix derived from the phylogenetic tree of the species as a random effect. The phylogenetic trees used in the analyses were obtained from BirdTree (<http://birdtree.org/>). We downloaded a posterior sample of 10 000 trees using the Hackett backbone for all species. For the MCMCglmm models, we randomly selected 1000 trees and generated a maximum clade credibility tree in TreeAnnotator v2.4.7 [54]. We used the following priors for the residual (R) and phylogenetic (G) variance in our models:

1. host status~nest architecture (binary trait distribution):  $R = (V = 1, \text{fix} = 1)$ ,  $G = (G1 = (V = 1E-10, \text{nu} = -1))$ . We also used a Gelman prior for the fixed effects (B) in this model
2. host-species richness~nest architecture (Poisson trait distribution):  $R = (V = \text{diag}(1), \text{nu} = 0.002)$ ,  $G = (G1 = (V = 1E-10, \text{nu} = -1))$ .

We ran all models for 27 500 000 iterations with 2 500 000 iterations as burn-in and a sampling interval of 5000. This allowed us to collect  $\gg 2000$  posterior samples of chains for estimating the model parameters, while also enabling us to keep the autocorrelation between stored iterations below 0.1 [55]. We assessed chain mixing and model convergence by visual inspection of the trace plots (electronic supplementary material, figure S1).

To investigate the evolution of host status and nest architecture (via two models: the first in-cavity versus any other nest architectures, and the second scrape versus all other nest architectures) in more detail, we used the methods for modelling trait coevolution across phylogenies as implemented in BayesTraits v3.0 [56,57]. We evaluated independent and dependent models using the 'Discrete' module of the software. We applied reverse jump MCMC estimations of the model parameters, with hyper exponential prior (RJHP0-1) where the mean was drawn from a uniform distribution between 0 and 1 [57,58], in two consecutive (independent) runs for each set including 100 randomly selected phylogenetic trees from the Hackett backbone of the Jetz *et al.* [59] global bird phylogeny used above. We set the chain length for each tree to 1 100 000 with 10% burn-in at the beginning of the chain, and when the process switched between trees, and sampled every 10 000 iterations, resulting in a total of 110 000 000 iterations and 10 000 posterior samples in each run for estimating the model parameters. We assessed convergence by applying Gelman and Rubin's convergence diagnostic [60,61]. Convergence is diagnosed when the outputs of independent MCMC chains are indistinguishable, i.e. the upper confidence limit of the 'potential scale reduction factor' converges to 1 [60]. These potential scale reduction factors were less than 1.02 (upper confidence limit < 1.07) and 1.01 (upper confidence limit < 1.05) for all parameters estimated in MCMC runs of the dependent and independent models of trait evolution, respectively. Despite this high level of convergence, a few parameters showed outlier estimates on a handful of tree topologies (electronic supplementary material, figure S2). To further investigate the cause of these irregularities, we repeated these coevolutionary analyses using a variety of other tree sources and settings.

In the cavity versus any other nest architecture classifications:

1. Hackett GeneOnly (4180 species), 10 000 posterior samples, RJHP0-1, dependent model

2. Hackett All Species (5787 species), 10 000 posterior samples, RJHP0-1, dependent model without forcing chains spending equal amount of iterations per each
3. Hackett All Species (5787 species), 10 000 posterior samples (every 15 000 were sampled with a total chain length of 16 000 000), RJHP0-1, independent model
4. Hackett All Species (5787 species), 10 000 posterior samples, hyper exponential prior where the mean is drawn from a uniform distribution between 0 and 5, independent model
5. Hackett All Species (5787 species), 10 000 posterior samples, exponential prior with a mean of 10, independent model
6. Hackett GeneOnly (4180 species), 10 000 posterior samples, exponential prior with a mean of 10, independent model
7. Ericson All Species (5787 species), 10 000 posterior samples, exponential prior with a mean of 10, independent model
8. Ericson GeneOnly (4180 species), 10 000 posterior samples, exponential prior with a mean of 10, independent model
9. Burleigh *et al.* [62] backbone with 100 ML bootstrap trees (3766 species), 10 000 posterior samples, exponential prior with a mean of 10, independent model
10. Prum *et al.* [63] backbone (135 species), 10 000 posterior samples (all on a single tree), exponential prior with a mean of 10, independent model.

In the scrape versus all other nest architecture classifications:

11. Hackett All Species (6207 species), 1000 posterior samples per each tree (a total of 100 000 posterior samples), RJHP0-1, both dependent and independent models, four independent MCMC runs, in BayesTraits v4.

As these results were all qualitatively identical to those of our original models, we present only a single set of models and report all other tree sources and model settings in electronic supplementary material, figures S3–S21.

Based on the models' marginal likelihoods estimated by a stepping stone sampler [64] using 100 stones iterated 10 000 times on each stone, we calculated the log Bayes Factors [65] between the complex (dependent) and simple (independent) models to test trait correlation during evolution. Log marginal likelihood values were first estimated for all 100 trees (electronic supplementary material, figure S22); and then, as a summary of the MCMC runs, we fitted the common probability distributions ( $n = 18$ , such as Cauchy's, Gaussian, Weibull's, uniform etc.) to the 100 log marginal likelihood values (after dropping the upper and lower 5%) to estimate a more accurate median value based on the parameters of the best-fitting distribution (the one with the lowest AIC value; electronic supplementary material, figure S23). The 'median' values measured as described above were used to calculate the log Bayes Factor for the two MCMC runs (see individual comparisons of log Bayes Factor by each tree in electronic supplementary material, tables S2–S3). The value of the log Bayes Factor indicates support for the complex model as follows:  $< -2$ —support for the independent model,  $-2$  to  $0$ —weak support for the independent model,  $0$  to  $2$ —weak support for the dependent model,  $2$  to  $5$ —support for the dependent model,  $5$  to  $10$ —strong support for the dependent model,  $> 10$ —very strong support for the dependent model [65]. Since this algorithm requires binary-coded traits, we therefore recoded the host status as being non-host (0) or host (1) and the nest architecture as being any type besides hole (0) or hole (1). Similarly, we binary-coded scrape nest architecture (0) or any other nest architectures (1) for a second round of analyses.

Finally, we applied stochastic character mapping of nest architecture simulated 1000 times under the ARD (all rates different) model available in the 'phytools' package [66,67], using the data of 5684 bird species to find the most likely ancestral nest type and visualize the most probable evolutionary transitions among the five nest architecture classes (see also electronic supplementary

material, table S4). We estimated Pagel's lambda ( $\lambda$ ) [68] by performing model fitting for discrete comparative data ('geiger' package [69,70]) to measure the phylogenetic signal in nest architecture. Data processing and visualization were performed in R v4.0.3 [71].

### 3. Results

#### (a) Nest accessibility and host status

Bird species building more open and accessible nests are generally more likely to be hosts to obligate avian brood parasites (figure 1a). More specifically, species building scrape ( $\beta = 1.51$ ,  $p < 0.001$ ), open cup ( $\beta = 1.46$ ,  $p < 0.001$ ) or dome nests ( $\beta = 1.04$ ,  $p < 0.001$ ) being more likely to be hosts than non-hosts. Meanwhile, there were no statistical differences in host status of species that build nests with domes and tubes ( $\beta = 0.25$ ,  $p = 0.504$ ), and hole-nesters showed a non-significant pattern of being less likely to be hosts ( $\beta = -0.51$ ,  $p = 0.077$ ).

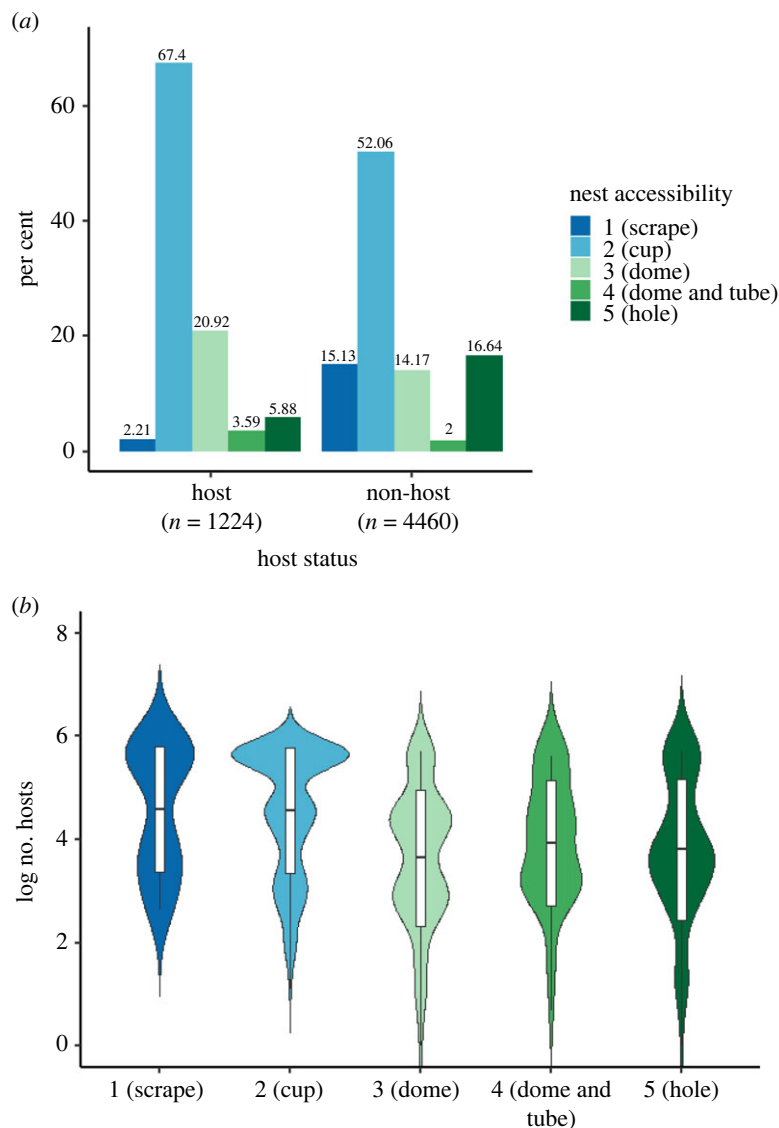
Based on the results of the stochastic-character mapping (figure 2), the most probable ancestral nest design of these 5684 bird species was a scrape nest (posterior probability = 0.97, 95% confidence interval: 0.96, 0.98). According to the best-fitting evolutionary model (log-likelihood =  $-2200.98$ , AICc = 4444.12), we estimated a strong phylogenetic signal ( $\lambda = 0.98$ ) in nest architecture, with a mean of 0.84 (95% confidence interval: 0.79, 0.89) based on the results of the top 150 fitted models (electronic supplementary material, table S1).

#### (b) Host-nest architecture and host specialization by parasites

Focusing on the dataset including host species only across all the different nest classifications, our results show that species building domed nests exhibit a non-significant trend towards being targeted by more specialist parasites ( $\beta = -0.20$ ,  $p = 0.089$ ). In turn, we found similar levels of parasite specialism among species building other nest types (scrape:  $\beta = -0.06$ ,  $p = 0.636$ , cup:  $\beta = 0.09$ ,  $p = 0.461$ , dome and tube:  $\beta = 0.01$ ,  $p = 0.966$ , hole:  $\beta = 0.06$ ,  $p = 0.649$ ) (figure 1b).

#### (c) Evolutionary transition analyses

Based on the results of the correlated-evolutionary analyses, host status and nest architecture have probably coevolved (in-cavity versus any other nest architectures: log Bayes Factor  $> 10$ ; see table 1a for more detail). Specifically, transitions from cavity nesting to non-cavity nesting have occurred on both host and non-host lineages, with higher rates in host lineages so that hosts were more likely to evolve to nest in more open nest types. Non-host status has more probably evolved in lineages of species that build their nests in cavities. More than 87% of the models supported correlated evolution of traits when we compared log marginal likelihoods of individual models estimated on the 100 randomly selected phylogenetic tree topologies, indicating a detectable role of correlated evolution between host status and nest architecture (as well as revealing the need to control for phylogenetic uncertainty in these models). According to the estimation of the character state of the common ancestor of all birds in this sample ( $n = 5787$ ), the ancestral state was probably non-hole nests, but with



**Figure 1.** The role of nest architecture in the coevolutionary dynamics of avian brood parasites and their hosts in relation to (a) the percentage of host and non-host species with nests of varying accessibility to brood parasites, with scrapes being the most accessible and holes being the least accessible, and (b) the accessibility of host nests in relation to the respective parasites' lowest host-species richness (host species only). The box plots indicate the 10th, 25th, 50th, 75th and 90th percentiles of the data distribution.

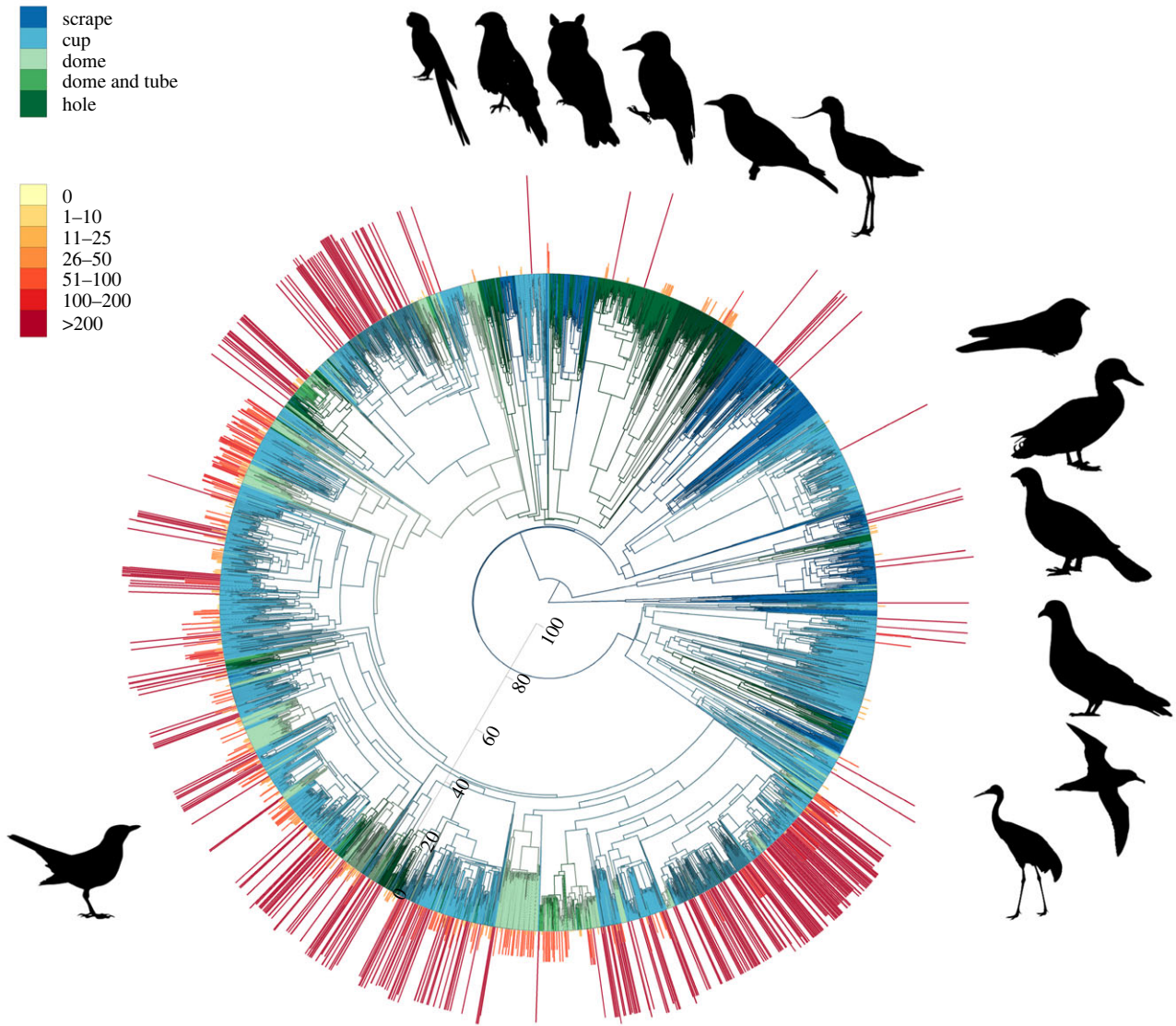
uncertainty between a non-host or a host status, with similar probabilities in both MCMC runs (approx. 0.45 and approx. 0.46, respectively; table 1a). The transition rates indicate that losses of brood parasitism were much more frequent for cavity than non-cavity nesting host lineages (figure 3).

Repeating this analysis to examine the coevolutionary relationship between host status and building a scrape nest (an especially accessible nesting strategy) also indicates robust evidence of coevolution between host status and nest architecture ( $n = 6207$  species; log Bayes Factor  $> 100$ ; table 1b). Specifically, transitions from scrape nesting to less parasite-accessible nest strategies occurred mainly on host lineages. Transitions from host to non-host status were more likely to occur in lineages with these less-accessible nest types. In this case, all models indicated the correlated evolution of these traits when we compared log marginal likelihoods of individual models estimated on the 100 randomly selected phylogenies, further supporting correlated evolution between host status and nest architecture. According to the estimation of the character state of the common ancestor of all birds in this sample, the ancestral state was

almost certainly scrape nest architecture and a non-host status (approx. 0.93 and approx. 0.94 in the two MCMC runs, respectively; table 1b); species then typically evolved to become non-hosts within lineages building more complex nest architectures or placing their nests in cavities (figure 4).

## 4. Discussion

We used phylogenetically informed comparative analyses and data from a large and global sample of bird species, including obligate brood parasites and their recorded hosts, to show that species with more accessible nests are more likely to be hosts than species with other, typically more enclosed types of nest architecture. Although some host species build enclosed and, thus, less accessible nests that serve as a front-line defence against parasitic species [35], these data show that obligate avian brood parasites, overall, target host species with more easily accessible nests. Meanwhile, we also confirmed recent findings [2] that host species with hole nests were targeted by more specialist



**Figure 2.** Phylogeny of 5684 species of birds indicating the results of stochastic character mapping of their main nest architecture (branch colours) and the respective parasites' lowest host-species richness (coloured bars).

brood parasites. Finally, the evolutionary-transition analyses showed that nest architecture has played a tractable role in the coevolutionary arms race between brood parasites and their hosts.

Obligate brood parasitic bird species appear to target those species that build open cup nests. Targeting host species with open cup nests is akin to brood parasites targeting species with poorer visual acuity, whereby hosts have relatively smaller eyes than non-hosts; this may mean that hosts are less able to spot foreign eggs in their nests [72]. Although parasites may target host species with open cup nests because those nests are relatively accessible to egg-laying females, it follows that open-nesting host species should be expected to employ other tactics to reduce their chances of being parasitized. For example, great reed warblers (*Acrocephalus arundinaceus*) construct their open-cup nests away from perches used by brood parasites to search for host activity [29], as well as in locations that are darker than random to prevent parasites from locating their nests [30]. Host species can, thus, reduce the chances of being parasitized by selecting inconspicuous nest sites which may also play an important role in shaping rates of brood parasitism. Nevertheless, the construction of open cup nests is unlikely

to be the only factor determining interspecific variation in parasitism rates because some heavily parasitized species, such as great reed warblers, continue to build open-cup nests that provide easy access for brood parasites.

Brood parasitic bird species also target host species building enclosed domed nests, but to a lesser extent than host species building open cup nests. As nest architecture likely provides a front-line defence against egg-laying brood parasites [25,35], then it is perhaps surprising that more host species have not evolved to build domed nests with long entrance tubes [35]. However, it may be that host species only evolve enclosed domed nests with long entrance tubes after they are targeted by brood parasites, so they are a further step in the ongoing coevolutionary arms race between brood parasites and their hosts [25].

It is also prudent to consider that our dataset is relatively coarse, and it may be possible that the relative body size of parasites and their hosts, and the size of the host nests may have further influenced the role of nest architecture in the ongoing arms race between parasites and their hosts. Consequently, in future studies it would be valuable to quantify the relative size of the host and parasite and nominate a given size differential whereby a dome or hole nest was likely to

**Table 1.** Summary of the two independent MCMC runs of the correlated evolutionary models with (a) in-cavity versus any other nest architectures and (b) scrape versus all other nest architectures.

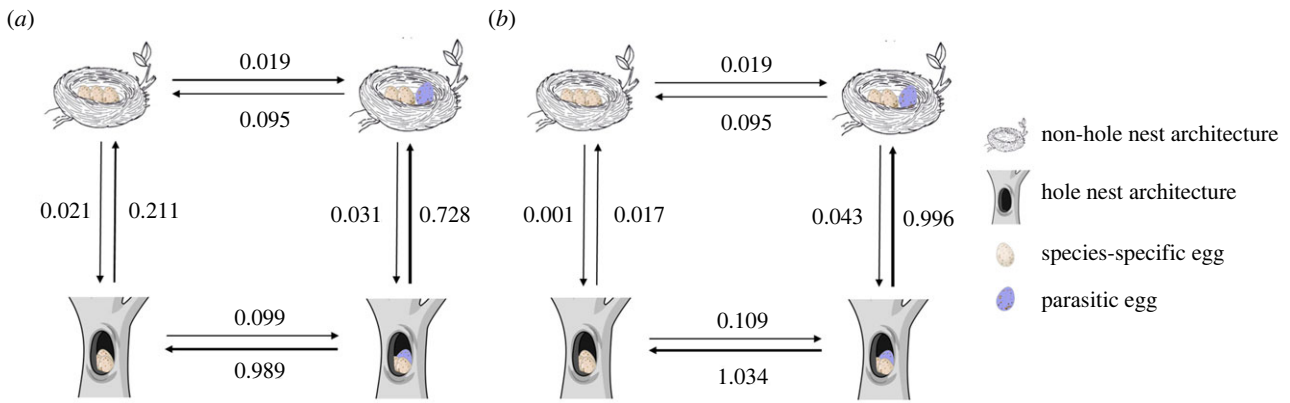
traits and transitions		dependent				independent				
host status	nest architecture	mean	lower 95% CI	upper 95% CI	log marginal likelihood (median)	transitions	mean	lower 95% CI	upper 95% CI	log marginal likelihood (median)
<i>(a)</i>										
MCMC run 1: log Bayes Factor = 11.22										
non-host	transition to hole	0.021	0.017	0.025	-3324.737	transition to host	0.014	0.014	0.014	-3330.348
non-host	transition to non-hole	0.211	0.172	0.249		transition to non-host	0.092	0.092	0.092	
host	transition to hole	0.031	0.027	0.034		transition to hole	0.001	0.001	0.001	
host	transition to non-hole	0.728	0.649	0.801		transition to non-hole	0.011	0.011	0.011	
transition to host	non-hole	0.019	0.019	0.019						
transition to non-host	non-hole	0.095	0.094	0.095						
transition to host	hole	0.099	0.089	0.108						
transition to non-host	hole	0.989	0.902	1.075						
root probability (non-host, non-hole)		0.446	0.444	0.448		root probability (non-host, non-hole)	0.449	0.449	0.450	
root probability (non-host, hole)		0.030	0.028	0.031		root probability (non-host, hole)	0.046	0.045	0.046	
root probability (host, non-hole)		0.478	0.477	0.479		root probability (host, non-hole)	0.459	0.458	0.459	
root probability (host, hole)		0.047	0.045	0.049		root probability (host, hole)	0.047	0.046	0.047	
MCMC run 2: log Bayes Factor = 13.91										
non-host	transition to hole	0.001	0.001	0.001	-3323.417	transition to host	0.014	0.014	0.014	-3330.370
non-host	transition to non-hole	0.017	0.016	0.018		transition to non-host	0.092	0.092	0.092	
host	transition to hole	0.043	0.038	0.047		transition to hole	0.001	0.001	0.001	
host	transition to non-hole	0.996	0.901	1.090		transition to non-hole	0.011	0.011	0.011	
transition to host	non-hole	0.019	0.019	0.019						
transition to non-host	non-hole	0.095	0.094	0.095						
transition to host	hole	0.109	0.099	0.119						
transition to non-host	hole	1.034	0.942	1.125						
root probability (non-host, non-hole)		0.441	0.439	0.443		root probability (non-host, non-hole)	0.449	0.448	0.449	
root probability (non-host, hole)		0.032	0.030	0.034		root probability (non-host, hole)	0.046	0.045	0.047	
root probability (host, non-hole)		0.477	0.476	0.478		root probability (host, non-hole)	0.458	0.458	0.459	
root probability (host, hole)		0.050	0.049	0.052		root probability (host, hole)	0.047	0.046	0.048	

*(Continued.)*

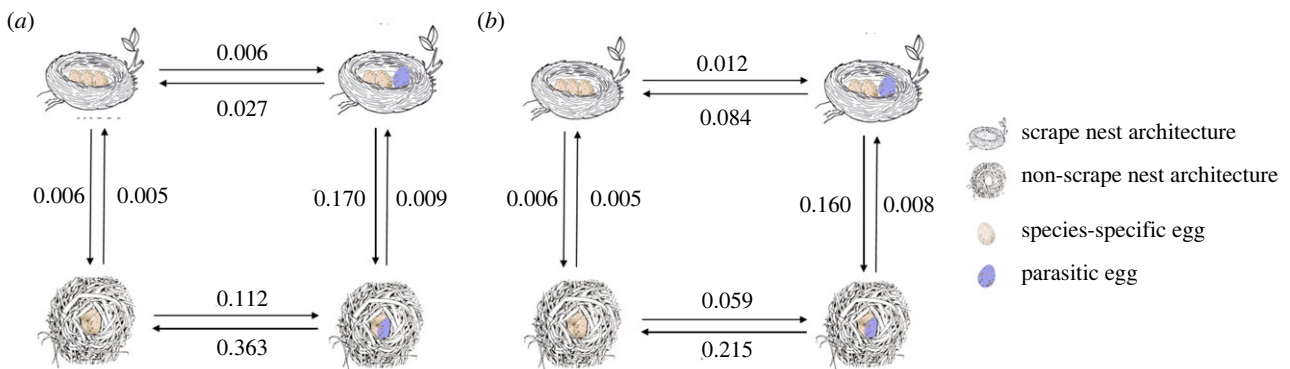
Table 1. (Continued.)

traits and transitions		dependent				independent				
host status	nest architecture	mean	lower 95% CI	upper 95% CI	log marginal likelihood (median)	transitions	mean	lower 95% CI	upper 95% CI	log marginal likelihood (median)
<i>(b)</i>										
MCMC run 1: log Bayes Factor = 117.93										
non-host	transition to non-scrape	0.006	0.006	0.006	-4534.797	transition to host	0.014	0.014	0.014	-4593.763
non-host	transition to scrape	0.005	0.005	0.005		transition to non-host	0.093	0.093	0.093	
host	transition to non-scrape	0.170	0.163	0.177		transition to non-scrape	0.012	0.012	0.012	
host	transition to scrape	0.009	0.009	0.010		transition to scrape	0.005	0.005	0.005	
transition to host	scrape	0.006	0.006	0.006						
transition to non-host	scrape	0.027	0.025	0.029						
transition to host	non-scrape	0.112	0.102	0.121						
transition to non-host	non-scrape	0.363	0.336	0.390						
root probability (non-host, scrape)		0.931	0.930	0.933		root probability (non-host, scrape)	0.457	0.455	0.459	
root probability (non-host, non-scrape)		0.024	0.024	0.024		root probability (non-host, non-scrape)	0.038	0.036	0.039	
root probability (host, scrape)		0.030	0.029	0.032		root probability (host, scrape)	0.467	0.466	0.469	
root probability (host, non-scrape)		0.015	0.015	0.015		root probability (host, non-scrape)	0.038	0.036	0.040	
MCMC run 2: log Bayes Factor = 127.60										
non-host	transition to non-scrape	0.006	0.006	0.006	-4532.015	transition to host	0.014	0.014	0.014	-4595.817
non-host	transition to scrape	0.005	0.005	0.005		transition to non-host	0.093	0.093	0.094	
host	transition to non-scrape	0.160	0.153	0.166		transition to non-scrape	0.012	0.012	0.012	
host	transition to scrape	0.008	0.007	0.008		transition to scrape	0.005	0.005	0.005	
transition to host	scrape	0.012	0.011	0.014						
transition to non-host	scrape	0.084	0.069	0.099						
transition to host	non-scrape	0.059	0.053	0.065						
transition to non-host	non-scrape	0.215	0.198	0.233						
root probability (non-host, scrape)		0.938	0.937	0.940		root probability (non-host, scrape)	0.456	0.454	0.457	
root probability (non-host, non-scrape)		0.029	0.029	0.030		root probability (non-host, non-scrape)	0.039	0.037	0.041	
root probability (host, scrape)		0.014	0.014	0.015		root probability (host, scrape)	0.466	0.464	0.468	
root probability (host, non-scrape)		0.018	0.018	0.019		root probability (host, non-scrape)	0.040	0.038	0.041	





**Figure 3.** Evolutionary transitions between pairs of trait states estimated by the discrete: dependent model using the nesting data of 5787 species: (a) MCMC run 1, (b) MCMC run 2 (see Methods). States of traits (clockwise, starting from the upper right corner): host (with parasitic egg) and any non-hole nest (1, 0); host and hole nest (1, 1); non-host (with only species-specific eggs) and hole nest (0, 1); non-host and any non-hole nest (0, 0).



**Figure 4.** Evolutionary transitions between pairs of trait states estimated by the discrete: dependent model using the nesting data of 6207 species: (a) MCMC run 1, (b) MCMC run 2 (see Methods). States of traits (clockwise, starting from the upper right corner): host (with parasitic egg) and scrape nest (1, 0); host and any non-scrape nest (1, 1); non-host (with only species-specific eggs) and any non-scrape nest (0, 1); non-host and scrape nest (0, 0).

be restrictive for the (typically larger) parasite; such an endeavour, however, would not be feasible on the large scale presented here. Nevertheless, our nest classifications are based on previously established functional classifications [25,35] and so represent a biologically meaningful approach. It is also worth considering that parasitism rates are usually low for a given population, but predation rates may well be much higher, and thus may be the primary determinant of nest design [36]. Nonetheless, our results to identify a signal of host status among parental species implies some detectable evolutionary impact of brood parasitism on host nest building strategies.

An alternative explanation is that nest type is subject to considerable phylogenetic inertia across nest-building avian lineages, a possibility supported by the observed overall low rates of different types of nest-structure transitions (figures 3 and 4). This was particularly apparent in the transitions between non-parasitized hole nests and non-parasitized non-hole nests and between parasitized non-hole nests and non-parasitized non-hole nests, which had no important evolutionary transitions. Thus, hosts may also adopt alternative strategies to guard against brood parasites.

Although most brood parasites target species nesting in open cup nests and enclosed domed nests, several brood parasites do target hole-nesting hosts (e.g. Europe [73,74]; the Americas [75]; Africa [76]). The evolutionary transition rates shown in figure 3 suggest that few species evolve to be hosts in hole nests. Nevertheless, greater honeyguides (*Indicator indicator*) parasitize little bee-eaters (*Merops pusillus*)

breeding in underground burrows with narrow entrance tunnels [76], and in Europe, common cuckoos lay eggs in hole-nesting common redstarts (*Phoenicurus phoenicurus*) [77]. When common cuckoos were unable to enter the redstarts' nest-boxes, they laid eggs in 31% of the observed 360 nests by pressing their cloaca up against the entrance hole before propelling an egg towards the nest cup [78]. Just one-third of such parasitism events, however, resulted in common cuckoo eggs within the nest cup, because most eggs were found on the rim of nests rather than in the nest cups. This meant that 31% of common redstart nests were parasitized, and the redstarts responded by deserting in 13% of cases, compared with lower desertion rates of 3% in non-parasitized nests [78]. Furthermore, when artificial non-mimetic common cuckoo eggs were placed in the redstart nests, 12% of them were rejected as the host parents deserted the nest, and when considering just the non-experimental cases of parasitism, just 21 (14%) common cuckoo offspring fledged from 150 eggs that were laid [78]. It seems, therefore, that parasitizing hole-nesting birds can present severe challenges for parasites [73].

Furthermore, brood-parasitic species may or may not become more specialist over evolutionary time [79], and it remains unclear whether hosts targeted by specialist brood parasites have had sufficient time to evolve enclosed nests [10,47]. The correlated evolutionary analyses conducted here showed that species were more likely to have evolved from being host species to being non-host species within lineages nesting in holes (as well as in scrapes). This confirms

that in the coevolutionary process between hosts and parasites, the arms race might end when nests become inaccessible for parasitism.

Host species building more easily accessible nests are more likely to be parasitized than species building other nest designs, which suggests both that parasites maximize their chances of successful parasitism events by targeting naive species with more easily accessible nests, and that other host species have evolved to build more enclosed nests to prevent parasites from laying eggs in their nests. Meanwhile, host species with enclosed nests were also targeted by more specialist brood parasites. Taken together, our results suggest that nest architecture plays an important role in both the initial and subsequent stages of the coevolutionary arms race between brood parasites and their hosts.

**Ethics.** There are no ethical considerations because this was a desk-based study.

**Data accessibility.** The data are provided in electronic supplementary material [80].

**Declaration of AI use.** We have not used AI-assisted technologies in creating this article.

**Authors' contributions.** M.E.H.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, supervision, validation, writing—original draft; J.N.: formal analysis, investigation, methodology, validation, writing—original draft,

writing—review and editing; C.S.: data curation, formal analysis, investigation, methodology, validation, writing—review and editing; N.D.A.: conceptualization, data curation, investigation, methodology, writing—review and editing; S.E.S.: data curation, formal analysis, investigation, methodology, validation, writing—review and editing; S.D.H.: data curation, investigation, methodology, supervision, validation, writing—review and editing; K.N.L.: data curation, investigation, methodology, supervision, validation, writing—review and editing; M.C.M.: investigation, methodology, validation, writing—original draft.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

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