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RESEARCH ARTICLE

Anthropogenic nest material use in a global sample of birds

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Abstract

As humans increasingly modify the natural world, many animals have responded by changing their behaviour. Understanding and predicting the extent of these responses is a key step in conserving these species. For example, the tendency for some species of birds to incorporate anthropogenic items—particularly plastic material—into their nests is of increasing concern, as in some cases, this behaviour has harmful effects on adults, young and eggs. Studies of this phenomenon, however, have to date been largely limited in geographic and taxonomic scope. To investigate the global correlates of anthropogenic (including plastic) nest material use, we used Bayesian phylogenetic mixed models and a data set of recorded nest materials in 6147 species of birds. We find that, after controlling for research effort and proximity to human landscape modifications, anthropogenic nest material use is correlated with synanthropic (artificial) nesting locations, breeding environment and the number of different nest materials the species has been recorded to use. We also demonstrate that body mass, range size, conservation status and brain size do not explain variation in the recorded use of anthropogenic nest materials. These results indicate that anthropogenic materials are more likely to be included in nests when they are more readily available, as well as potentially by species that are more flexible in their nest material choice.

KEYWORDS
artificial material, bird nests, conservation, nest material, plastics

1 | INTRODUCTION

The Earth's now over eight billion human inhabitants have left a significant mark upon the natural world (Crist et al., 2017; Venter et al., 2016). Many non-human animals (hereafter 'animals') currently live within or in close proximity to human-modified landscapes, and some have remarkable morphological or behavioural adaptations to such conditions (Alberti, 2015; McDonnell & Hahs, 2015; Palumbi, 2001). While a number of species thrive in anthropogenic settings (e.g. the success of urban red foxes, Plumer et al., 2014; or the persistence of threatened parrots within cities, Luna et al., 2018), others have experienced rapid population declines or local extinctions (McKinney, 2008). The ability to understand and therefore predict species' response to urbanisation and other human modifications would thus improve our ability to protect and conserve species vulnerable to such changes (Dornelas et al., 2014; Marzluff, 2001; McDonald et al., 2008; McGill et al., 2015).

The nest is key to the reproductive success of nearly all bird species (Collias & Collias, 2016; Hansell, 2000). A well-constructed nest will protect the eggs and young from predators and environmental

pressures (Deeming & Reynolds, 2016; Mainwaring & Hartley, 2013; Reid et al., 2000), and the materials used to construct a nest can reflect various physical and mechanical properties known or thought to contribute to offspring survival (Bailey et al., 2014, 2016; Breen et al., 2021).

Some bird species are known to incorporate anthropogenic (human-made) materials into their nests (reviewed in Jagiello et al., 2019, 2023; Reynolds et al., 2019). This phenomenon has ranged from a 1933 record of a pied crow (known then as *Corvus scapulatus*, now *Corvus albus*) placing various wire pieces into a 20-lb nest (Warren, 1933) to reports of plastic debris in 12% of nests in 14 northwest European seabird species (O'Hanlon et al., 2021) and in up to 100% of yellow-legged gull (*Larus michahellis*) nests in Barcelona (Galimany et al., 2023). Anthropogenic materials sometimes appear to provide benefits, such as the reduction of ectoparasites in the nest due to the inclusion of cigarette butts by house sparrows (*Passer domesticus*) and house finches (*Carpodacus mexicanus*) (Suárez-Rodríguez et al., 2013). In other cases, the inclusion of such material into nests is known or presumed to be harmful; the incorporation of plastics into seabird nests, for example, puts individuals at higher risk of entanglement or ingestion (Gall & Thompson, 2015; Huin & Croxall, 1996; Montevecchi, 1991; O'Hanlon et al., 2021), and the same plastic string that strengthens great grey shrike (*Lanius excubitor*) nests in Poland also kills nestlings and breeding females (Antczak et al., 2010).

Most studies of anthropogenic nest material use to date have focused on a small number of species and/or have had limited geographic scope. For example, in addition to the aforementioned studies, anthropogenic nest materials have been studied in great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) in Warsaw, Poland (Jagiello et al., 2022); in black kites (*Milvus migrans*) in Doñana National Park in Spain (Sergio et al., 2011); and in Chinese bulbuls (*Pycnonotus sinensis*) in Hangzhou, China (Wang et al., 2009). Determining whether the patterns of anthropogenic nest material use found in these studies generalise across all taxa and/or ecological settings, however, would be an important step in assessing the conservational consequences of this behaviour as well as for predicting what additional species might either already use or soon begin to adopt anthropogenic material.

A recent study of anthropogenic nest material use in 125 species of birds (Jagiello et al., 2023) identified two potential correlates of interspecific variation in the extent of this phenomenon: dome nesting and sexual body mass dimorphism, with birds that build domes and/or have generally larger males than females less likely to incorporate anthropogenic material. They found no evidence within this sample that anthropogenic nest material correlated with any other nesting variable (type, habitat, component), life-history trait (longevity, fecundity, developmental mode), range size, bill size, brain size, proximity to human landscape modification, mating system or sex of the nest builder; moreover, several models (on different sample sizes and with different combinations of predictor variables) indicated that the correlations with dome nesting and/or sexual dimorphism were in fact not statistically significant. A larger and more diverse sample size might thus help to clarify the statistical interpretation of some of these potential evolutionary relationships.

We began by reviewing the literature on anthropogenic material use and identifying five key sets of potential ecological and evolutionary drivers of broad-scale interspecific variation in anthropogenic nest material use. The first, and most straightforward, is *proximity to human-modified environments* (i.e. the accessibility of anthropogenic materials), which has been demonstrated in many population-level studies (e.g. Bond et al., 2012; Jagiello et al., 2019; Lopes et al., 2020; O'Hanlon et al., 2021; Suárez-Rodríguez et al., 2013) but was not identified as a statistically significant correlate in the aforementioned comparative study of 125 species (Jagiello et al., 2023).

The second potential set of drivers focuses on the *general availability of nest materials* (Briggs & Deeming, 2016; Mennerat et al., 2009), as one might expect that an unusual or potentially harmful anthropogenic material would be more likely to be successfully incorporated when other (more preferred) materials are scarce. As this phenomenon would be difficult to measure on the scale of thousands of species, we propose that this theme could be very broadly captured at the level of terrestrial biome, with, for example, tropical forests generally more likely to contain suitable natural nest material than deserts.

The third attempts to capture the *energetic constraints of the nests* themselves. Different nest construction strategies are assumed to have different energetic demands (Mainwaring & Hartley, 2013), and thus a bird constructing a nest of new materials (as opposed to excavating or co-opting a cavity, or lining a scrape, Jagiello et al., 2023), requiring a large volume of materials (e.g. a dome as opposed a cup) or requiring materials with specific structural properties (e.g. a dome or a cup as opposed to a platform or a lined scrape) may be more likely to incorporate any available material, even if of anthropogenic origin. We note that Jagiello et al. (2023) found no support for this prediction; indeed, they found that birds that build dome nests were *less* likely to incorporate anthropogenic materials. This might indicate that the material and behavioural specialisation necessary to construct a dome is incompatible with the flexibility necessary for a species to construct with an anthropogenic material of uncertain or inadequate structural properties. It is furthermore possible that body size could serve as a proxy for some of these species-level energetic constraints, with smaller species requiring proportionally more energy to build the same type of nest and thus being potentially more likely to turn to anthropogenic materials.

Our fourth set of drivers centres on *behavioural flexibility*; species that are less constrained in their material choice by cognitive or mechanical limitations (Hansell, 2007) and/or with higher levels of neophilia may be more likely to interact with and incorporate anthropogenic materials. One proxy for this concept might be the number of nest materials the species has been recorded as using, with large numbers of materials indicating fewer constraints on material choice and thus a potential increased opportunity to incorporate anthropogenic materials. This variable would, of course, be highly sensitive to research effort, as would many of the other variables and traits

mentioned here (Stutchbury & Morton, 2001; Xiao et al., 2017). Additionally, several authors have suggested that larger brained species might be more likely to incorporate anthropogenic material (Jagiello et al., 2023; Lefebvre et al., 2004; Sol et al., 2002, 2008, 2014), perhaps due to a potential link between relative brain size and neophilia, though the exact mechanism underlying this pattern is not yet understood (Healy, 2021).

Finally, our fifth set of drivers focuses on the potential *conservation importance* of this behaviour. As discussed above, the use of anthropogenic nest material has been documented as detrimental to individual survival, and yet is becoming increasingly common. The ability to understand and predict anthropogenic nest material use beyond a handful of especially well-studied systems would be of particular interest. For example, it is currently unknown if this behaviour covaries with conservation status (i.e. if endangered species are more or less likely to have been recorded incorporating anthropogenic material); the answer to this question might guide future studies of anthropogenic nest material. In particular, given that anthropogenic nest material may indicate tolerance towards humans and of other environmental perturbations more broadly (see the paragraph on flexibility above), it is possible that this behaviour is primarily the purview of ecological generalists. While range size is an imperfect proxy for ecological specialisation (especially for seabirds), it is thus possible that—after controlling for research effort—species with larger ranges are more likely to incorporate anthropogenic material. Such a correlation could help guide conservation efforts; we note, however, that Jagiello et al. (2023) found no relationship between range size and anthropogenic nest material use in their sample of 125 species.

To address these five sets of potential evolutionary drivers, and to test whether correlations found within small numbers of species can be generalised across the avian tree of life, we present a global database of recorded nest materials ($n = 6147$ species across 223 families), scored for the documented use of anthropogenic material. We then use Bayesian phylogenetic comparative methods to evaluate potential ecological, environmental and conservation correlates of anthropogenic nest material use across these species, selecting potential predictor variables related to these potential explanatory themes. Due to particular concerns about plastics, given their non-biodegrading nature and the harm plastic entanglement and ingestion causes to birds (e.g. Avery-Gomm et al., 2018; O'Hanlon et al., 2021; Townsend & Barker, 2014), we also separately consider the use of plastics as nest material within our data set.

2 | MATERIALS AND METHODS

2.1 | Data collection

Available descriptions of nest materials were collated from three sources: the Handbook of the Birds of the World Alive (HBW; 2017–2018), Neotropical Birds Online (NBO; 2019–2020) and the Birds of North America Online (BNA; 2019–2021); note that subsequently all of these sources have been combined into a single resource, the Birds of the World (Billerman et al., 2022). These lists of materials were then scored as a binary trait for the presence of anthropogenic material, which included string, rope, fishing line, wire, aluminium foil, cloth, paper, rubbish/trash, concrete fragments, cellophane, etc. We included all materials manipulated by the bird and used in the construction of the nest within these lists, including materials used as nest lining (though not including materials placed during the construction process but then removed prior to egg laying); this was primarily because the authors of these sources rarely differentiated among the various structural functions of nest materials, but also because we had no a priori hypotheses to test regarding potentially different functions of materials used in different structural components of the nest.

Additionally, we separately scored these lists for the presence of plastic material; note that this variable may be underdocumented even within the context of these lists of nest materials, as some poorly-specified materials such as 'rubbish' maybe have in fact contained plastics but could not with certainty be determined as plastic use. For each species, we also recorded the total number of different nest materials used (i.e. the number of distinct material types listed, as separated by a comma, the word 'or' or the word 'and'); if a species had multiple entries across the three sources, the maximum number of materials per source was taken as the species value.

We note that these lists of nest materials, like any record of a behaviour in the wild, will vary in completeness; this is of particular relevance to the incorporation of anthropogenic and plastic nest materials, as this phenomenon has increased over time and will almost certainly continue to do so. We control for this to the best of our ability by using a proxy variable for research effort, as detailed below.

Nest structure and location were also scored based on HBW, NBO and BNA entries and photographs. Structure was marked as presence–absence for no nest or a scrape (i.e. no constructed nest, but material used as liner); a platform; a cup; a dome (including multi-chambered dome-and-tube nests); and an excavated nest (including nests where a cavity is excavated and then a nest is constructed inside). Location was marked as presence–absence for an artificial location (e.g. nest boxes, telephone poles, house eaves, etc.); on the ground or touching water; inside an earthen or tree cavity; on or within rocks raised above the ground; and attached to vegetation (e.g. reeds, bushes, trees). Uncertainty in nest categorisation—either noted in the entry itself (e.g. 'dubious record') or due to coder interpretation (e.g. an unclear description or photograph)—was regarded as trait absence, and disagreement between sources was resolved in favour of trait presence. Subsets of the six researchers coding nest structure and location ('coders') met regularly to discuss questions and spot-check each other's work, and approximately one-third of entries were later checked by at least one of the two most experienced coders. All coders followed a detailed data collection manual and had a

formal biological background (one undergraduate student, one post-baccalaureate researcher, one Masters student and three postdoctoral researchers).

Body mass and range size data were obtained from Sheard et al. (2020). Brain size data were taken from the volume compilation published in Hooper et al. (2022) and averaged for a single per-species value; given that body mass is included as a covariate within these models, it can be interpreted as relative brain size. IUCN 2020 Red List status was obtained where possible from BirdLife International (IUCN, 2022) on 7 November 2022 and then, for the handful of species exhibiting taxonomic mismatches, scored manually from the IUCN Red List website (https://www.iucnredlist.org/). To improve the accuracy of our parameter estimates, and as we had no a priori biological reason to distinguish these particular categories, we reclassified 'endangered' species to include both endangered and critically endangered species; 'extinct' species to include species both extinct and extinct in the wild; and 'threatened' species to include near threatened and vulnerable species. Species with a conservation status of 'data deficient' were considered as missing information, and thus were excluded from any analyses containing conservation status as a predictor variable.

Biome membership was scored by intersecting the 2018 BirdLife International range maps (BirdLife International, 2018) with the World Wildlife Fund (WWF) global terrestrial biome data (Olson et al., 2001) and taking as the biome identity for each species the biome with the greatest proportional intersection; birds with majority non-terrestrial ranges were scored as 'seabirds' and a few birds were hand-scored according to IUCN Red List habitat information and/or Birds of the World habitat information due to taxonomic mismatches or errors with the range maps. The WWF biomes known as 1, 2 and 3 were considered 'tropical forests'; biomes 4 and 5 were considered 'temperate forests'; biomes 6 and 11 were combined into a single tundra-taiga category; biomes 7, 8, 9 and 10 were considered 'grasslands'; biome 12 was considered 'Mediterranean'; biome 13 was considered 'desert'; biome 14 was considered 'mangroves' (see Table S1 for more information on the biome definitions and coding). As a measure of proximity to human landscape modification, a per-species score for the commonly used human footprint index (HFI, a global score from 0 to 100 on each terrestrial square kilometre measuring the human impact on the landscape, such as urbanisation, farmland, roads, etc.—see, e.g. Jagiello et al., 2019) was calculated by intersecting the Human Footprint Index (Wildlife Conservation Society, 2005) with a 1°×1° grid and finding the average value for each grid cell, multiplying these values as a vector across a presence–absence grid for the world's birds based on the 2018 BirdLife International range maps, and then calculating the arithmetic mean for each species. Finally, as many of these variables are likely to covary with the amount of scientific investigation of each species' ecology, we recorded the number of articles returned by a Web of Science search of each scientific name (12 January 2023 to 23 January 2023) as a proxy for research effort.

As this was a computational study resulting from secondary sources of data, no ethics approval was required.

2.2 | Phylogenetic comparative methods

To test for the associations between anthropogenic/plastic nest material use and the proposed explanatory variables, we fitted Bayesian phylogenetic logistic regressions using the package *MCMCglmm* (Hadfield, 2010) in R version 4.1.3 (R Core Team, 2022). We controlled for phylogenetic autocorrelation due to the shared evolutionary history of the species in our data set; this specific approach was selected instead of other phylogenetic regression strategies due to the ability to integrate our results over a distribution of phylogenies, thus accounting for phylogenetic uncertainty within our models, and to perform logistic regressions. Anthropogenic and plastic nest material use were each considered as binary response variables; fixed effects were all included within a single model to reduce Type I error and to control for covariation between these possible predictors. So as to avoid granting undue influence to extreme outlying values, body mass was log-transformed and research effort square-root transformed prior to analysis, and to improve model coefficient interpretability, the continuous variables of material number, body mass, range size, research effort and human footprint index were each rescaled to have a mean of 0 and a variance of 1. A sample of 100 phylogenetic trees was obtained from the Hackett backbone of the Global Bird Tree (Jetz et al., 2012), trimmed to match the data from each model, and included as random effects within each model. Note that species missing any data (from the predictor variables or the phylogeny) were omitted from the analysis.

Priors for the fixed effects were determined using Gelman priors (command 'gelman.prior', Gelman et al., 2008), with the prior for the phylogenetic variance set to $V = 1^{-10}$ and $\nu = -1$ and with the residual variance fixed to 1 (see supplementary methods and/or published code for more information). For each of the two models (anthropogenic and plastic material use), an initial 'dummy' run was used to determine a start point on an arbitrary tree topology for 11,000 iterations, with a burn-in of 1000 and a sampling rate of 10. We then looped across each of the 100 tree topologies for 30,000 iterations for each tree, with a burn-in of 10,000 and a sampling rate of 2000, for a total of 10 stored iterations per tree. MCMCglmm provides 'pMCMC values', somewhat analogous to statistical significance, consisting of twice either the probability that coefficient $\beta < 0$ or the probability that coefficient $\beta > 0$, whichever is smaller; we report these, along with the 95% credible interval for the fixed effect parameter estimates for each predictor tested.

Trace plots of model outputs were visually inspected to ensure convergence and proper mixing, and all effective sample sizes in the main two models were greater than 475. To ensure that correlation between the fixed effects were not affecting the accuracy of parameter estimates, we checked variance inflation factors using code published in Sheard et al. (2020); all values were found to be below 6. Sample autocorrelation for the fixed and random effects was assessed using the function 'autocorr' and determined to be less than 0.2. For the full version of the model (i.e. that presented in Tables 1 and 2), we further ensured model convergence by running a total of three independent chains per model and calculating the

TABLE 1 Results of a Bayesian phylogenetic mixed model predicting interspecific variation in anthropogenic nest material use.

	Coefficient	Lower 95% CI	Upper 95% CI	ESS	pMCMC
Research effort	0.344	0.098	0.570	1000	0.004
# Materials	1.739	1.478	2.081	605	<0.001
Body mass	−0.682	−1.702	0.171	753	0.142
Range size	0.035	−0.205	0.266	913	0.760
HFI	0.479	0.196	0.774	1061	<0.001
Conservation—extinct	−1.739	−8.283	4.229	1000	0.664
Conservation—LC	−0.701	−1.831	0.352	1000	0.216
Conservation—threatened	−0.917	−2.241	0.471	1000	0.196
Biome—grasslands	−1.080	−1.799	−0.381	1000	0.002
Biome—Mangroves	−2.535	−8.695	3.625	1000	0.434
Biome—Med.	−0.984	−2.216	0.279	1000	0.124
Biome—Marine	−0.872	−2.761	0.847	1017	0.356
Biome—Taiga/Tundra	−1.297	−2.335	−0.047	1000	0.020
Biome—Temperates	−1.591	−2.487	−0.773	967	<0.001
Biome—Tropics	−2.318	−3.083	−1.531	1000	<0.001
Nest structure—scrape/none	−0.418	−1.779	0.878	1000	0.528
Nest structure—cup	−0.767	−2.007	0.409	776	0.192
Nest structure—platform	−0.184	−1.545	1.391	1000	0.790
Nest structure—dome	−0.644	−2.005	0.553	775	0.316
Nest structure—excavation	0.033	−1.514	1.701	933	0.970
Nest location—artificial	1.878	1.241	2.472	1000	<0.001
Nest location—ground/water	−0.124	−0.818	0.618	1000	0.734
Nest location—cavity	−0.331	−1.241	0.478	1000	0.494
Nest location—elevated rock	−0.207	−0.983	0.547	1124	0.580
Nest location—vegetation	0.070	−0.823	0.912	882	0.870

Note: Coefficients above 0 indicate a positive correlation with anthropogenic nest material use within a multivariate framework; coefficients below 0 indicate negative correlation. Conservation parameters are compared with a baseline of endangered species; breeding biome parameters are compared with a baseline of desert location. As many species nest in multiple structures and locations, these are included in the model as separate binary variables rather than as single categorical variables. Statistically significant coefficients are highlighted in grey.

Abbreviations: CI, credible interval; ESS, effective sample size; HFI, human-footprint index; LC, least concern; Med., Mediterranean.

Gelman–Rubin statistic (Gelman & Rubin, 1992), a measure of convergence of multiple MCMC chains; all potential scale reduction values were below 1.1, indicating that all three runs converged on the same set of answers. We also performed posterior predictive checks and estimated a pseudo-R^2 value using code published in Nakagawa and Schielzeth (2013). Further information on model evaluation can be found in Supporting Information.

These models containing all potential correlates of anthropogenic and plastic material use (i.e. research effort, number of materials, body mass, range size, HFI, conservation status, biome membership, nest structure and nest location) contained fewer species ($n = 4237$) than our total sample of all species with both nest material and phylogenetic information ($n = 5960$). We therefore employed model selection procedures on both sets of response variables as sensitivity analyses, to verify that our results were robust to larger sample sizes. In brief, we sequentially compared the DIC fit between our main model and versions run on the same sample with individual statistically non-significant fixed effects removed; at each iterative step, if any newly accepted model could be performed on a larger sample of species, this model was re-run and this larger sample considered at the subsequent model selection step. We halted this procedure when either we found the best-fitting model according to DIC fit or when all statistically non-significant variables had been removed from the model.

We were able to obtain brain size data for only a small subset of our sample ($n = 760$); so as not to limit the evaluation of all other possible predictor variables to only this subset (which is presumably taxonomically and geographically biased), we considered the potential relationship between brain size and anthropogenic/plastic nest material within a separate set of models.

We also estimated the phylogenetic signal in both anthropogenic and plastic nest material use using the Fritz and Purvis *D* statistic for binary traits (Fritz & Purvis, 2010); a *D* statistic of 0 indicates a distribution consistent with Brownian motion, and a statistic of 1 indicates a distribution random with respect to phylogeny (with a

TABLE 2 Results of a Bayesian phylogenetic mixed model predicting interspecific variation in plastic nest material use.

	Coefficient	Lower 95% CI	Upper 95% CI	ESS	pMCMC
Research effort	0.482	0.223	0.736	847	<0.001
# Materials	1.141	0.855	1.378	597	<0.001
Body mass	−0.960	−2.366	0.218	476	0.100
Range size	−0.129	−0.433	0.166	674	0.410
HFI	0.569	0.190	0.908	675	0.004
Conservation—Extinct	−1.182	−7.880	5.343	1370	0.794
Conservation—LC	−0.542	−2.054	0.879	1000	0.450
Conservation—Threatened	−0.931	−2.843	0.886	1000	0.300
Biome—Grasslands	−1.255	−2.317	−0.091	1000	0.026
Biome—Mangroves	−1.510	−7.890	4.615	1000	0.692
Biome—Med.	−0.577	−2.678	1.193	1000	0.556
Biome—Marine	−0.788	−2.768	1.194	1000	0.456
Biome—Taiga/Tundra	−0.411	−1.724	1.069	1000	0.558
Biome—Temperates	−1.301	−2.524	−0.177	1000	0.018
Biome—Tropics	−1.000	−2.123	0.034	899	0.070
Nest structure—scrape/none	1.644	0.135	2.931	1000	0.022
Nest structure—cup	−0.211	−1.559	1.183	1198	0.764
Nest structure—platform	1.339	−0.171	2.796	1000	0.072
Nest structure—dome	0.363	−1.194	1.665	1224	0.604
Nest structure—excavation	−0.878	−3.184	1.617	1000	0.464
Nest location—artificial	1.143	0.368	1.916	717	0.004
Nest location—ground/water	−0.311	−1.236	0.629	1000	0.482
Nest location—cavity	−0.402	−1.366	0.813	1000	0.476
Nest location—elevated rock	0.214	−0.736	1.142	1000	0.648
Nest location—vegetation	0.221	−0.749	1.280	1223	0.718

Note: Coefficients above 0 indicate a positive correlation with plastic nest material use within a multivariate framework; coefficients below 0 indicate negative correlation. Conservation parameters are compared with a baseline of endangered species; breeding biome parameters are compared with a baseline of desert location. As many species nest in multiple structures and locations, these are included in the model as separate binary variables rather than as single categorical variables. Statistically significant coefficients are highlighted in grey.

Abbreviations: CI, credible interval; ESS, effective sample size; HFI, human-footprint index; LC, least concern; Med., Mediterranean.

statistic below 0 indicating greater phylogenetic conservation than expected under Brownian motion and a statistic above 1 indicating greater overdispersion than expected under a random model). The values were calculated by a set of 1000 permutations, run on a random tree from the posterior distribution.

Further details about the model specifications can be found in the published code and in Supporting Information.

3 | RESULTS

Of the 7148 nest material entries that we were able to obtain (including several instances of multiple entries per species), 327 entries mentioned anthropogenic nest material (and 102 entries mentioned plastic material). While anthropogenic and plastic nest material did show some phylogenetic signal, their distribution was not consistent with a Brownian motion model of evolutionary change ($D=0.69$ for anthropogenic material and $D=0.82$ for plastic material). According to the Birds of the World taxonomy, these entries combine to a count of 6147 species, of which 291 (4.7%) were documented as building nests with anthropogenic material and 92 (1.5%) with plastic material (Figure 1). The orders with the highest proportion of species that have been observed incorporating anthropogenic nest material include the Coraciiformes (kingfishers, bee-eaters, motmots; 1 of 6 species, 17%), the Ciconiiformes (storks; 3 of 20 species, 15%), the Falconiformes (falcons and caracaras; 2 of 16 species, 13%) and the Suliformes (gannets, cormorants, frigatebirds; 6 of 48 species, 13%); the orders with the highest proportion of observed plastic material use included the Suliformes (5 of 48 species; 10%), the Strigiformes (owls; 1 of 16 species, 6%) and the Pelecaniformes (pelicans, herons, ibises; 4 of 100 species, 4%).

Note that the BirdTree (Jetz et al., 2012) taxonomy, on which the phylogenetic models were based, contains fewer species than the Birds of the World, and thus, the comparative models were based on at most 5960 species, of which 282 were recorded to use anthropogenic material and 90 to use plastic material.

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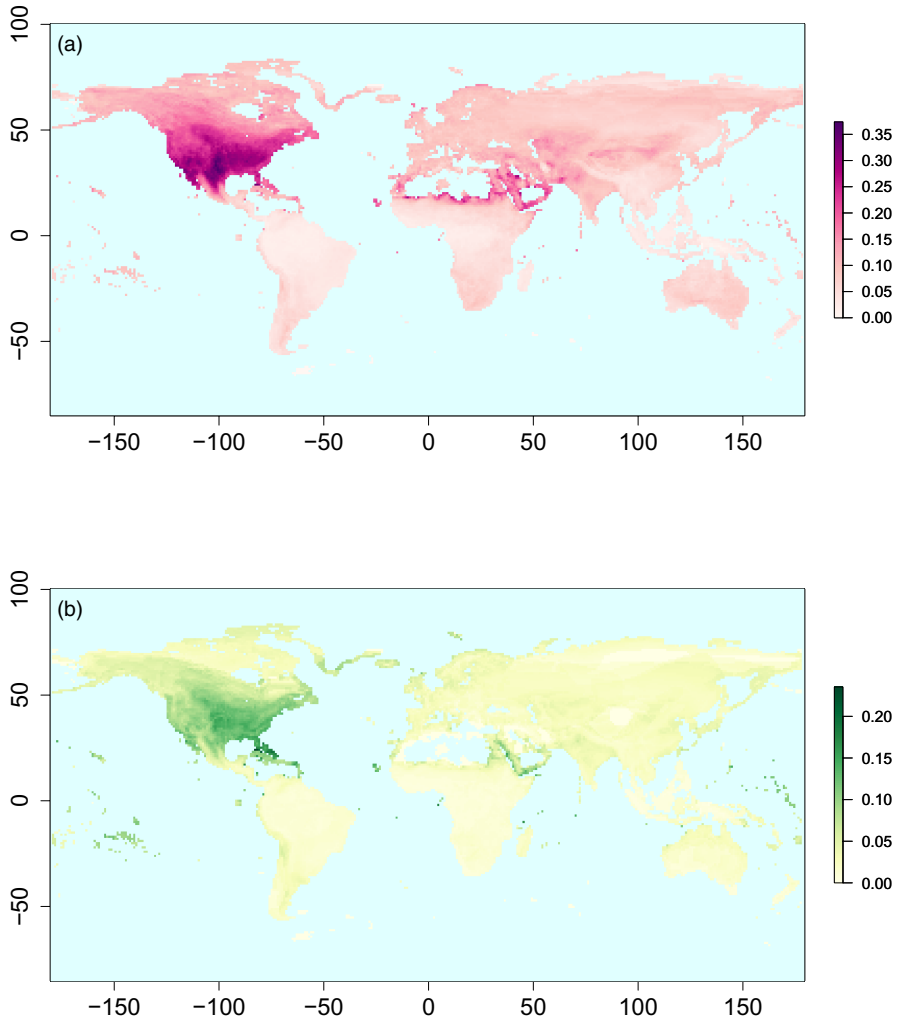

FIGURE 1 Global distribution of recorded anthropogenic and plastic nest material use. Darker colours indicate greater proportions of recorded anthropogenic (purple, panel a) and plastic (green, panel b) nest material use among the species breeding there, at the 1°×1° scale. Locations with fewer than 20 species with recorded nest material use (e.g. interior Greenland, Sahara Desert) have been omitted for ease of interpretation. Unlike the results of the phylogenetic models, these maps show the data uncorrected for English language research effort—that is, birds breeding in the English-speaking Global North are likely to be better represented than birds breeding elsewhere.

Globally, after controlling for a positive effect of research effort (β=0.344, *pMCMC*=0.004; Table 1; Figure 2) and proximity to human-modified landscapes (β=0.479, *pMCMC*<0.001), species were more likely to incorporate anthropogenic materials into their nests if they nest in synanthropic (human-modified) locations (β=1.878, *pMCMC*<0.001) and/or are documented as incorporating greater numbers of different materials into their nests (β=1.739, *pMCMC*<0.001). The tendency to incorporate anthropogenic nest material also varies by biome membership; after controlling for the effects of research effort and human modification, the inclusion of anthropogenic nest material is highest in deserts, lowest in tropical forests and intermediate in grasslands, taiga/tundra and temperate forests. There are no significant correlations between anthropogenic material use and body mass, nest structure, range size or IUCN conservation status. The model selection procedure supported this full model, despite the inclusion of non-significant variables (Table S2), and posterior predicted checks showed a good correspondence of observed to predicted values. The estimated pseudo-R^2 value for this model was 0.918.

Bird species that use plastics in their nests also tended to nest in synanthropic (human-modified) locations (β=1.143, *pMCMC*=0.004; Table 2; Figure 3) and/or were recorded as incorporating more types of materials into their nests (β=1.141, *pMCMC*<0.001), after controlling for the positive effect of research effort (β=0.482, *pMCMC*<0.001) and human landscape modification (β=0.569, *pMCMC*=0.004). Species were also more likely to have been recorded as using plastics in their nest if they use materials only for lining, without constructing full nest structures (i.e. were scored as using 'scrapes' or 'no nest'; β=1.644, *pMCMC*=0.022), and plastic incorporation was less common in grasslands and in tropical forests than in other biomes. As with anthropogenic materials, plastic nest material use was apparently not related to body mass, range size or conservation status. Model selection procedures again supported this full model, despite the inclusion of non-significant variables (Table S3), posterior predictive checks suggested good model fit and the estimated pseudo-R^2 value for this model was 0.884.

We found no evidence that relative brain size, proposed by some to be a potential proxy of cognitive performance and neophilia (e.g. Lefebvre et al., 2004, but see Healy, 2021), correlates with either anthropogenic or plastic material use (anthropogenic: β=1.081, *pMCMC*=0.126, Table S4; plastic: β=0.117, *pMCMC*=0.848, Table S5).

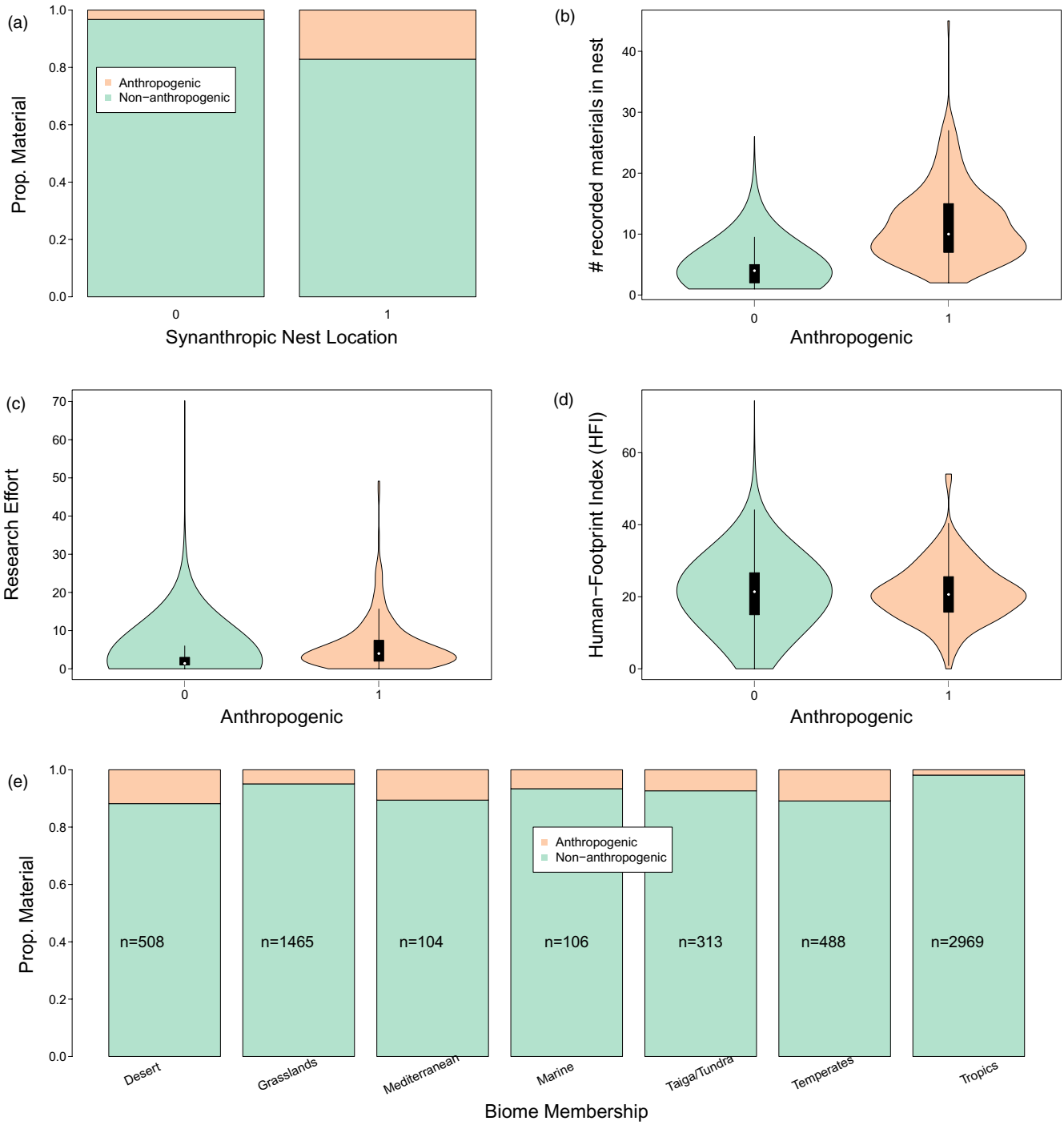

FIGURE 2 Ecological and synanthropic correlates of anthropogenic nest material use. Frequencies, uncorrected for phylogenetic signal or covariance with any other predictor, are presented at the species level between species that are (peach) and are not (green) known to use anthropogenic nest material and (a) species that are and are not known to nest in synanthropic locations, (b) the number of nest materials recorded for each species, (c) 'research effort', here estimated by the number of papers indexed by the Web of Science about that species, (d) the average human footprint index for that species and (e) assigned biome membership. For ease of display in panel (e), the seven species that breed predominantly in mangroves have been omitted, and all columns have been labelled with the number of species in each category. All patterns displayed are statistically significant in the phylogenetically-corrected model after controlling for multiple covariates (see Table 1). Prop., proportion.

4 | DISCUSSION

We have demonstrated that bird species that incorporate plastic and anthropogenic materials into their nests are—after controlling for research effort and proximity to human landscape modifications—more likely to nest in synanthropic (human-modified) locations and to incorporate more types of material into their nests, compared with species that are not known to use plastic/anthropogenic nest materials.

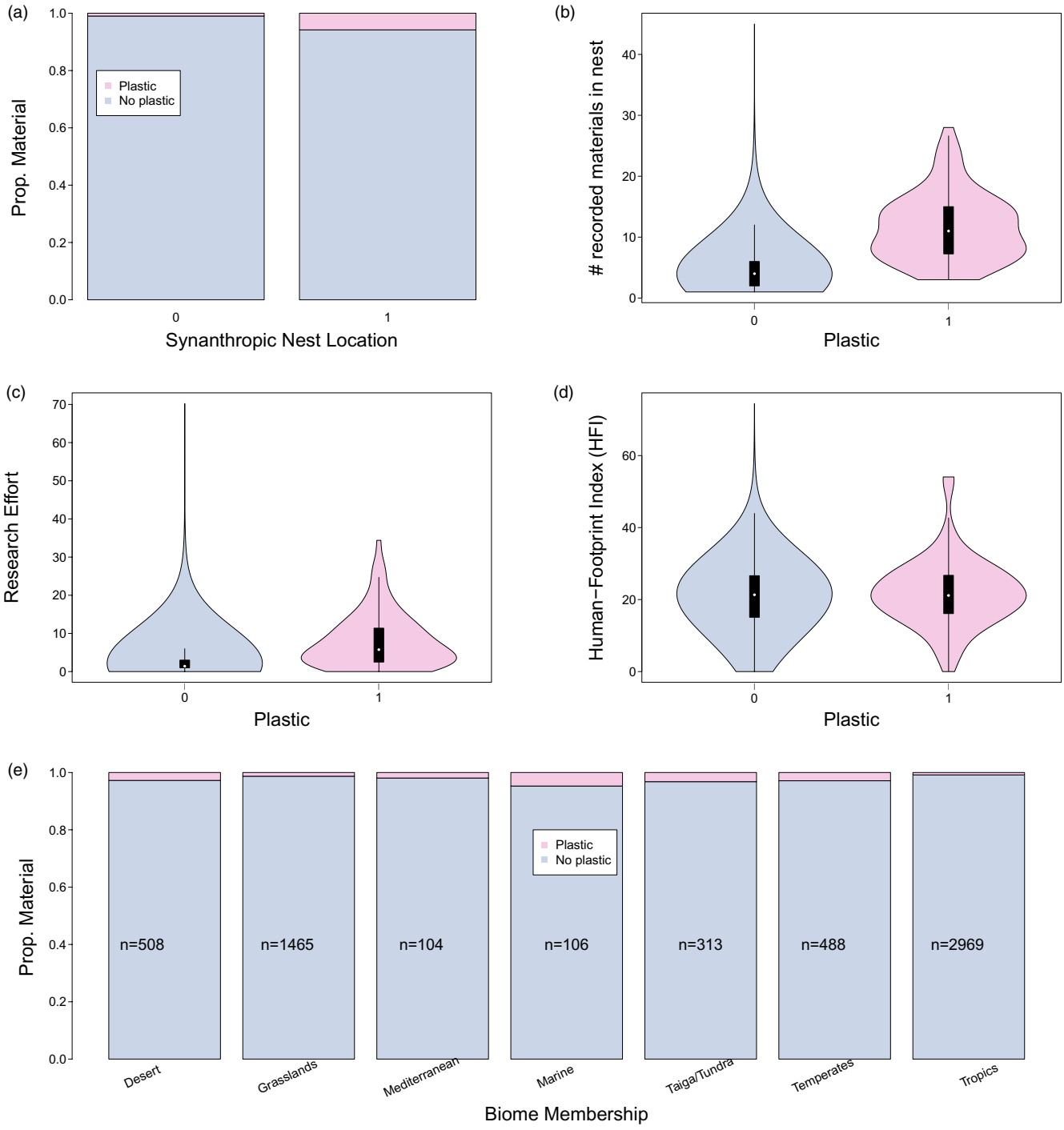

FIGURE 3 Ecological and synanthropic correlates of plastic nest material use. Correlations, uncorrected for phylogenetic signal or covariance with any other predictor, are presented at the species level between species that are (pink) and are not (purple) known to use anthropogenic nest material and (a) species that are and are not known to nest in synanthropic locations, (b) the number of nest materials recorded for each species, (c) 'research effort', here estimated by the number of papers indexed by the Web of Science about that species, (d) the average human footprint index for that species and (e) assigned biome membership. For the purposes of displaying panel (e), species that breed predominantly in mangroves have been omitted, and all columns have been labelled with the number of species in each category. All correlations shown are statistically meaningful within a phylogenetically corrected, multivariate framework (see Table 2). Prop., proportion.

We have also demonstrated variation in anthropogenic and plastic material use between major breeding biomes; for example, anthropogenic nest material use was highest in deserts and the lowest in the tropics.

Within our models, species that are associated with heavily human-modified landscapes (have a higher human footprint index, HFI) and/or that nest in human-modified locations (e.g. nest-boxes,

telephone poles, roofs, etc.) are more likely to incorporate both anthropogenic material in general and plastic material specifically into their nests. This indicates that the inclusion of anthropogenic and plastic material into nests is potentially related to the availability of these materials (Breen et al., 2021; Hansell, 2000). Our interspecific comparative data also confirm previous intraspecific correlations between anthropogenic nest material use and either HFI (e.g. Jagiello et al., 2019) or other measures of human proximity (e.g. Antczak et al., 2010; Townsend & Barker, 2014; Wang et al., 2009) (though see Jagiello et al., 2023, who found no relationship between HFI and anthropogenic nest material use in a sample of 125 species of birds).

This correlation between anthropogenic nest material use and the ability to breed in human-modified habitats does not, however, seem to extend to a general high tolerance of a wide variety of ecological niches, as there is no relationship between anthropogenic/plastic material use and range size. In particular, this result could potentially suggest that species that use anthropogenic/plastic material are not necessarily ecological generalists, which given the different responses of generalists and specialists to habitat loss or changing climate might in turn have important conservation implications (Kuussaari et al., 2009; Soga & Koike, 2013; Stuart-Smith et al., 2021). Further study with more targeted measures of ecological niche size—particularly those that distinguish between marine and terrestrial species—might clarify this relationship.

The suggested relationship between anthropogenic material use and material availability is further bolstered by the associations we found between anthropogenic/plastic material use and breeding biome. Anthropogenic nest material use is most prevalent in desert regions, where other types of nest material might be scarce, and is rare in tropical forests, which typically contain high amounts of biomass and somewhat lower amounts of human modification. This interpretation would accord with the data from individual bird populations, which show that nest material use is constrained by material availability (Alvarez et al., 2013; Briggs & Deeming, 2016), and that collecting nest material (e.g. searching, carrying) is energetically costly (Mainwaring & Hartley, 2013; Surgey et al., 2012). Potentially, this result could suggest that the incorporation of anthropogenic material may allow birds to breed successfully in areas where nest materials are uncommon, such as deserts, and thus possibly implies a beneficial effect of incorporating anthropogenic materials (see, e.g. Seco Pon & Pereyra, 2021, for a study of anthropogenic nest material use in kelp gulls). That there is no overall correlation between anthropogenic material use and range size in this data set, however, would indicate that such an advantage might be limited, perhaps only to certain clades or ecological contexts.

Our analyses also suggest a potential secondary driver of anthropogenic nest material use: flexibility. Across our large sample of species, species recorded as using a higher number of nest materials are more likely to use both anthropogenic material generally and plastic material specifically. This pattern could be rooted in several causes, including fewer constraints on materials for properties such as thermal insulation (Windsor et al., 2013) or sexual signalling (Jagiello et al., 2023; Sergio et al., 2011); higher levels of neophilia (Greenberg & Mettke-Hofmann, 2001); or a cognitive (Sugasawa et al., 2021) or mechanical (Sheard et al., 2023) propensity to interact with more types of materials. A species that builds nests using a wider range of materials might thus be more likely to effectively incorporate anthropogenic materials, especially those with properties not easily replicated in nature. This relationship is apparently independent of our proxy for research effort, though caution is warranted, as the number of English-language research articles indexed by Web of Science under one of potentially several synonymous scientific names does not of course fully encapsulate the total human knowledge about a species' nest material use. Future comparative studies of smaller taxonomic groups might consider more targeted proxies of research effort. Intriguingly, however, the relationship between anthropogenic nest material use and the number of recorded materials is also independent of interspecific variation in relative brain size, a trait which some have found to correlate with neophilia and success in novel (although not necessarily urban) environments (Lefebvre et al., 2004; Sol et al., 2002, 2014). While this finding might in part be a consequence of the smaller sample size of the brain size models, the lack of correlation might also suggest, unsurprisingly, an imperfect relationship between recorded material use, neophilia and brain size across the world's birds (Healy, 2021).

Other than the tendency for species that use materials solely for lining (but do not excavate cavities or construct walled nests, the 'scrape/none' category of nest structure) to be more likely to incorporate plastic into these linings, we observed no differences in anthropogenic/plastic material use among species that build different nest types, nor among species with different body masses. Gathering materials is assumed to be energetically costly (Collias & Collias, 2016; Hansell, 2000; Mainwaring & Hartley, 2013), with different nest designs potentially bearing different costs, and the effects of these costs are expected to vary allometrically with body size; there is, however, no quantitative data yet available on these hypotheses. If anthropogenic items were a non-preferred material, they might be expected to appear more frequently in more material-heavy nests (i.e. in domes or cups instead of scrapes) or in the nests of species less able to pay metabolic costs (i.e. of smaller birds); we find no such pattern. This may in part reflect the diversity of physical properties of these 'anthropogenic' materials, as the costs and benefits of building a nest containing, for example, nails (as documented in the familiar chat, *Oenanthe familiaris*) might be substantially different from those of building a nest containing, for example, string.; an analysis examining the relevant material properties of these anthropogenic materials might be able to detect a clearer relationship between material use and energetic costs.

Despite the increasing body of literature indicating individual-level harmful effects of the inclusion of anthropogenic materials into bird nests (Antczak et al., 2010; Carbó-Ramírez et al., 2015; O'Hanlon et al., 2021; Suárez-Rodríguez et al., 2017; Suárez-Rodríguez & Macías Garcia, 2014), we found no correlation at the species level between the incorporation of anthropogenic/plastic materials and conservation status. This may indicate that anthropogenic material

use is not necessarily a current major threat to threatened and endangered species. Given the limitations in our understanding of the potential benefits and harms of anthropogenic nest material use, and given the strong correlation between research effort and the probability of detecting anthropogenic nest material use in our data, however, we urge caution in over-interpreting this result.

As human modifications to the natural world proliferate, we will also see increased animal behavioural responses to these changes. Whether a species is able to react in the short term to these habitat modifications, and whether these responses are ultimately adaptive, is an important question in understanding and mitigating the effects of the Anthropocene (Mainwaring et al., 2017). Our demonstration that one specific response, that is, the inclusion of anthropogenic materials into bird nests, is apparently a by-product of both material availability and nest material flexibility thus underscores the importance of understanding the ecological and evolutionary origins of traits related to these behavioural consequences of human habitat modifications.

AUTHOR CONTRIBUTIONS

CS designed the study. CS, SES and LS collected and collated the data, with guidance from KNL, SDH and SS. CS and LS performed the analyses. CS wrote the paper, and all authors contributed writing and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data and code underlying this study can be found at https://doi.org/10.5281/zenodo.10719750 (Sheard et al., 2024).

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SUPPORTING INFORMATION

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

Figure S1: Trace and density plots for the fixed and random effects of the phylogenetic logistic regression predicting recorded anthropogenic nest material use (see Table 1).

Figure S2: Trace and density plots for the fixed and random effects of the phylogenetic logistic regression predicting recorded plastic nest material use (see Table 2).

Figure S3: Predicted versus observed nest material use for anthropogenic (above, green, $R^2 = 0.92$) and plastic (below, purple, $R^2 = 0.85$) materials.

Figure S4: Distributions of simulated model data (light blue, 'y') and observed data (dark blue, 'yrep') for the full model predicting anthropogenic nest use.

Figure S5: Distributions of simulated model data (light blue, 'y') and observed data (dark blue, 'yrep') for the full model predicting plastic nest use.

Table S1: Terrestrial biome definitions.

Table S2: Model selection procedures for anthropogenic nest material use.

Table S3: Model selection procedures for plastic nest material use.
Table S4: Results of a Bayesian phylogenetic mixed model predicting interspecific variation in anthropogenic nest material use, with brain size as an additional predictor.
Table S5: Results of a Bayesian phylogenetic mixed model predicting interspecific variation in plastic nest material use, with brain size as an additional predictor.
Data S2: Data supporting the results presented in this study.

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