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Why do some bird species incorporate more anthropogenic materials into their nests than others?

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Abstract

Many bird species incorporate anthropogenic materials (e.g. sweet wrappers, cigarette butts, plastic strings) into their nests. Anthropogenic materials have become widely available as nesting materials in marine and terrestrial environments globally. These human-made objects can provide important benefits to birds such as serving as reliable signals to conspecifics or protecting against ectoparasites, but they can also incur fundamental survival and energetic costs via offspring entanglement and reduced insulative properties, respectively. From an ecological perspective, several hypotheses have been proposed to explain the use of anthropogenic nest materials (ANMs) by birds but no previous interspecific study has tried to identify the underlying mechanisms of this behaviour. In this study, we performed a systematic literature search and ran phylogenetically controlled comparative analyses to examine interspecific variation in the use of ANM and to examine the influence of several ecological and life-history traits. We found that sexual dimorphism and nest type significantly influenced the use of ANMs by birds providing support for the 'signalling hypothesis' that implies that ANMs reflect the quality of the nest builder. However, we found no support for the 'age' and 'new location' hypotheses nor for a phylogenetic pattern in this behaviour, suggesting that it is widespread throughout birds.

Keywords: nest materials, nest type, nests, phylogenetically controlled comparative analysis, plastic

1. Introduction

Nests are built by a range of vertebrate and invertebrate taxa, including fish, reptiles, insects, amphibians, birds and mammals [1]. These structures determine the conditions in which their offspring develop and, thereby, are fundamental to their reproductive success [1–3]. Therefore, the materials constituting nests are fundamental to offspring development (e.g. thermal stability, antiparasitic properties; [4]) and survival (e.g. nest concealment; [5]). Nest materials are also important for reproduction in other contexts such as sexual selection [6]. Among all nest-building animals, birds are probably the taxon about which nest-building behaviour is best understood; as such, they represent excellent model systems to understand in greater detail the ecological significance of nest construction by animals generally.

Nest-building birds use a wide variety of natural materials such as twigs, grasses, mosses, feathers or leaves (e.g. [1]). However, there is mounting evidence that they also use anthropogenic nest material (ANM) such as plastic strings, cigarette butts and fragments of plastic bags (figure 1a; [8,9]). This article will summarize our current knowledge of this apparently novel behaviour and explain why birds use ANMs in their nests from an ecological perspective.

(a) The incorporation of anthropogenic material into birds' nests

At first glance, the incorporation of ANMs into nests appears to be a novel phenomenon in birds with an increasing number of studies published in recent years (e.g. see [9] and references therein). However, this behaviour by birds was observed from as early as the 1830s [10] with first reports published in 1933 (e.g. [11]). That said, its prevalence has undoubtedly increased recently [12,13]. A repeated survey of a Danish colony of black-legged kittiwakes (*Rissa tridactyla*) showed that whilst ANMs were found in 39.3% of 466 nests examined in 1992, it had increased to 57.2% of 311 nests in 2005 [14]. Møller [15] found that the prevalence of plastic in common blackbird (*Turdus merula*) nests in Danish farmland had increased since the 1950s when it was first recorded through to the 1970s, when plastic coverage of farm crops such as potatoes (*Solanum tuberosum*) and silage reached its peak. Potvin *et al*. [10] examined 893 nests of 224 bird species held in Australian museums and found that whilst 4% of nests collected in 1832 contained ANM, this had increased to nearly 30% by 2018. They put this temporal increase in ANMs down to increased incorporation of more persistent synthetic material compared to more biodegradable nest constituents. Synthetic material was first detected in a nest examined from Melbourne in 1956 [10].

The use of ANMs in birds' nests appears to be very widespread among taxa. Current evidence indicates that many seabird nests contain ANM [14–19]. Nests of urban birds regularly contain ANMs such as cigarette butts, pieces of cotton and fragments of plastic bags [10,20–24, reviewed by 9]. On intensively managed farmland, ANMs such as plastic string, fragments of the liner used to cover bales and other agricultural items are also found in nests [7,17,25–30]. The composition of natural materials in nests varies interspecifically and intraspecifically [26]. We expect similar variation in the use of ANMs by birds exposed to different ecological forces. While Reynolds *et al*. [9] reviewed nest structure and composition within an urbanization context, summarizing the hypotheses for the use of ANMs by urban birds, to date, no previous study has attempted to synthesize current knowledge on the topic in birds generally. Currently, we lack even basic information about the diversity of ANMs in bird nests and an exhaustive list of species using them. Such basic information is crucial to explain intra- or interspecific patterns in ANM use by birds, thereby allowing identification of species predisposed to such behaviour. This compilation, based on a systematic literature review, and presentation of this descriptive information is the first objective of our study. Our systematic literature review then allows us to address our second objective: the critical evaluation of the trade-off between benefits and costs of using such materials. The potential costs and benefits of the ANM incorporation by birds into their nests have also been overlooked in the literature to date. These are crucial before hypotheses can be framed to investigate the ecological forces shaping this behaviour. Finally, our third objective is to test several previously proposed hypotheses within an analtyical framework underpinned by interspecific (phylogenetically controlled) comparisons.

(b) Hypotheses explaining interspecific variation in anthropogenic nest material use

There are several hypotheses that have been proposed that may be equally applicable to other (non-avian) nest-building animal taxa. Here, we describe the principal hypotheses that could explain interspecific variation in nest-building behaviour as well as associated predictions.

The 'availability hypothesis' (AVH) [24,31] proposes that the most commonly available materials in the nesting environment are used by birds to construct their nests. The AVH is supported by two main facts: (i) the local availability of natural nesting materials affects nest composition [32]; and (ii) ANMs are increasingly present in the environment. Solid waste material production currently amounts to > 2 billion tonnes per year, but it is expected to increase by more than 50% by 2050 [33]. This high production rate combined with the persistence of plastic and other synthetic materials implies that potential ANMs are constantly accumulated in marine and terrestrial environments globally [33–35]; thus, they are increasingly available for nest building. There may, however, be variation in the degree to which ANMs are available to nest-building birds because materials such as plastic are much more persistent in the environment than many others. Such variation in their persistence may mean that ANMs such as plastic may appear to be collected more often by birds than other materials, at least in nests that are used over repeated seasons. Nevertheless, several observational studies have found a positive association between the presence of environmental solid waste materials in the vicinity of nests and the ANMs in them [7,36]. Bond *et al*. [37] found such a positive relationship in northern gannet (*Morus bassanus*) nests in which reductions in ANM content coincided with the closure of a nearby fishery, with there being no such changes at a site further away from the fishery. Similarly, patterns in ANM usage by common blackbirds reflected those of plastic usage on agricultural fields in Denmark [15]. Probably the most convincing support for the AVH is provided by an experimental study involving black-faced spoonbills (*Platalea minor*) that modified nest composition following manipulation of the availability of artificial and natural materials in the vicinity of their breeding colony [38]. A previous study including data from 19 bird species [39] found a positive association between the prevalence of ANMs in nests and the Human Footprint Index (HFI), a proxy for anthropogenic pressures on the environment [40]. However, this study did not control for species' ancestry (i.e. phylogeny) and thus, its findings are not conclusive. Considering that the species' likelihood of finding potential ANMs increases with their distributional range, we predict a positive association between species' use of ANMs in their nests and their distributional range.

The 'age hypothesis' (AGH) [28] proposes that the use of ANMs in breeding attempts by birds increases with the age of the nest builder. To date, this hypothesis has received equivocal support from, on the one hand, several investigations finding an age effect of ANM usage in nests of two long-lived species, black kites (*Milvus migrans*) and white storks (*Ciconia ciconia*) [7,28]. On the other hand, no such evidence was found in great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) [21]. Jagiello *et al*. [21] concluded that interspecific differences in longevity between species might explain mixed support for the AGH with breeding experience of long-lived focal species contrasting markedly with shorter-lived ones. However, weak support for the AGH in some studies might be underpinned by methodological limitations such as difficulties in ageing some focal species [21]. Thus, an interspecific study examining the relationship between longevity and ANMs is needed to test this hypothesis rigorously. According to the AGH, we predict that species living longer are more likely to incorporate ANMs into their nests due to nest-building experience accrued during previous breeding attempts [9].

The 'new location hypothesis' (NLH) [22] proposes that nest composition changes because of the placement of nests in new sites. This hypothesis is based on studies showing that several bird species living in human-transformed habitats (e.g. cities) use non-natural nesting substrates such as window canopies or chimneys to breed rather than vegetation [24,41; reviewed in 9]. These new sites impose different restrictions on nest-building traits such as choice of nest attachment actions than do natural substrates. According to the NLH, we would expect that the incorporation of ANMs would be detected in structural, as opposed to lining, components of nests. Therefore, we predict an influence of nest type (e.g. burrow *versus* dome nests) in interspecific comparisons of ANM usage. Likewise, we predict that nesting substrate or habitat type (e.g. natural *versus* human-modified such as urban areas) will heavily influence ANMs in nests with birds breeding in the latter experiencing greater availability of ANMs [9].

Finally, the 'signalling hypothesis' (SH) [28] proposes that the use of ANMs is important for sexual selection and thus, birds will use them as an extended phenotype to indicate their 'quality' through nest building, as nests are also considered an extended phenotype in nest-building animals [42]. The use of ANMs has been previously described within this sexual selection context in bowerbirds (Ptilonorhynchidae) [43] in which males use items such as plastic caps of specific colours to decorate female-attracting bowers. Sergio *et al*. [28] again provided support for the SH through observations that black kite pairs that included larger amounts of white plastic in their nests were also those 'performing' better according to multiple 'quality' indices. In contrast, ANMs in species such as song thrushes (*Turdus philomelos*) do not appear to fulfil this function [44]. In interspecific comparisons, we predict a strong positive association between the intensity of sexual selection and the occurrence of ANMs. In species with strong sexual selection a non-bodily ornament is more likely to be selected for when its costs (e.g. predation risk) are decoupled from its benefits (e.g. increased fitness) [42].

2. Methods

(a) Literature search

We conducted an extensive bibliographic search in both Web of Science and Scopus to find all peer-reviewed studies published until July 2022. The combination of terms used in our search was: ("anthropogenic" OR "synthetic" OR "artificial material*" OR "waste" OR "debris" OR "litter*" OR "rubbish*" OR "garbage") AND ("nest*") AND ("bird*" OR "avian"). From 2 771 papers identified, we removed duplicates from the two literature databases and then followed a selection procedure based on title, abstract and full text screening (figure S1; [45]). We retained only those studies that included detailed information about the usage of ANM (i.e. the type and number of ANMs in nests). We added seven papers to our database because four were found in the **References** sections of papers found in our literature search, and three were published after July 2022 and detected by co-authors. Our literature search yielded 94 papers, 19 of which were excluded because six were literature reviews (and included data already presented in the other papers) and 13 did not provide complete datasets on ANMs. In summary, our final database included 75 papers providing relevant information about usage of ANMs by 176 species in 34 608 nests.

(b) Metadata compilation

Using the papers identified in §2a, we created a database including information on the use of ANM in each species. We extracted the type and number of different ANMs used based on the classification used by the CSIRO Global Leakage Baseline Project [46]. This detailed classification includes 51 subcategories grouped into five categories (i.e. plastic, paper, cloth, metal and other) that have been used in similar studies [21]. We also compiled the following information from each selected study: (1) study species; (2) single/range of year(s) of study; (3) latitude; (4) longitude; and whether birds had (5) become entangled in or (6) ingested ANMs in nests. Latitude and longitude allowed us to identify (7) the nesting habitat where the study took place and to classify land type as coast, island, natural, rural or urban. In addition, we extracted the (8) HFI of an area (HFI2km) prescribed by a 2-km radius around each study's location. This variable is a quantitative measure of the degree of human disturbance in a study area [40] and is associated with specific predictions of the AVH (see §1b).

We also collected information from the original papers on (9) the nest component (i.e. lining, structure, both or no information) in which the ANM was found. These data are related to the predictions of the NLH (see §1b).

We collected additional information on several ecological and life-history traits for each of the species included in our database from different available sources. We used *Birds of the World* [47] to obtain the following variables: (10) nesting substrate, grouped into grass/reeds, ground, ground hole/cavity, ledge, tree/bush, tree hole/cavity, water or wall; (11) nest type, classified into bed, burrow, cup, dome, plate or scrape; (12) sex of the nest builder (male, female or both); and (13) mating system (monogamy, polygyny or promiscuous). The first two were chosen as important for testing predictions of the NLH while the latter two are associated with those from the SH (see §1b).

Data on (14) clutch size were obtained from global [47] or regional compilations or from species-specific papers when not available in the former. We used the average clutch size when a range of values was provided in various sources. Data on (15) developmental mode (altricial, precocial, semi-altricial) were retrieved from the same global or regional compilations as previously described. If unavailable in the published literature, we looked for online images showing nestlings to classify them into one of these three categories. We followed a similar procedure to obtain data on (16) fecundity (the number of breeding events per year). These variables (14–16) are important to control for reproductive investment/restrictions in our analyses. Information on (17) migratory status (migrant or resident) was compiled from global databases such as Birdlife.org and *Birds of the World* [47] as well as from specific papers [48]. Following recommendations from these specialized papers, we considered a species as migratory if it was described as a partial or latitudinal migrant. We used the AVONET database [49] to extract information on (18) species' distributional ranges (km^2). These two variables (17,18) are important to test the predictions of the AVH (see §1b).

We compiled (19) longevity data (i.e. maximum number of years in the wild) from different online databases such as AnAge (https://genomics.senescence.info/species/index.html), Euring (https://euring.org/) or the Australian Birds and Bat Banding Scheme (https://www.dcceew.gov.au/science-research/bird-bat-banding) as well as from published datasets. This information is important to test the predictions of the AGH (see §1b).

We used Dunning [50] to obtain data on male and female body masses that were used to calculate (20) sexual dimorphism as male body mass minus female body mass. This value has been used previously and provides a continuous variable of the male-female variation in body mass with positive and negative values indicating relatively larger males and females, respectively. This variable is particularly important to test the predictions of the SH (see §1b).

Using AVONET [49], we also retrieved data on bill depth (mm) and bill length (mm) of each species that were then used to calculate the (21) bill index [51]. This variable was important to consider in relation to morphological constraints in some species in the potential incorporation of some ANMs. Finally, we obtained data on (22) relative brain size from Fristoe *et al*. [48] that was important when considering cognitive constraints in some species in exhibiting certain behaviours associated with the manipulation of ANMs.

(c) Statistical analyses

We used the database created in §2b to perform phylogenetically controlled comparative analyses to examine the interspecific variation in the use of ANMs. First, we totalled records of ANMs of each category to create a new variable (i.e. 'All') that represented a species' willingness to use any kind of ANMs (i.e. the higher the count, the more evidence available for the use of ANMs). Given that on average almost 60% of ANMs was plastic (see §3), we decided to create another new variable (i.e. 'Plastic') that included all records from the plastic ANM category. Secondly, we calculated the variance inflation factor (VIF) for all predictors before fitting the models (*usdm* package, [52]), and excluding predictors with VIFs >2 to avoid multicollinearity problems [53]. Thirdly, we applied the generalised linear mixed model (GLMM) approach with Bayesian Markov Chain Monte Carlo method

(*MCMCglmm* package, [54]) to fit our models. We ran separate models for 'All' and 'Plastic' as our response variables, controlling for the phylogeny of species and including multiple records of the same species such as for the yellow-legged gull (*Larus michaellis*), the data for which came from three different studies (table S1). Bird phylogenetic trees were obtained from BirdTree (http://birdtree.org), from the source of 'Hackett All Species', and a maximum clade credibility tree was generated from 1 000 randomly selected trees in TreeAnnotator v2.4.753 [55]. The resultant consensus tree was used during model fitting. We followed a backward selection procedure based on *p* values to simplify our full models. We first fitted a full model entering all predictors without multicollinearity problems and then reduced it by eliminating the predictor with the highest *p* value step-by-step, until reaching a minimal model containing only predictors with *p* values < 0.10. We fitted zero-inflated Poisson regression for the 'All' models but a binary logistic regression for 'Plastic' models due to the poor fitting of zero-inflated Poisson regression to the data and thus, the dichotomisation of the variable (0 – non-users, 1 – users). We used a Gelman-prior [56] for the fixed effects (B) and G=(G1=(V=1E-10, nu=-1), G2=(V=1E-10, nu=-1)) priors for the phylogenetic variance in our models. We applied R=(V=diag(2), nu=0.002, fix=2) and R=(V=1, fix=1) settings for the residual variance in the Poisson and logistic regressions, respectively.

To maximize the number of records (n = 237, 125 species), we first excluded predictors containing >20% of missing values ('All' and 'Plastic' models). After this initial filtering, the predictors of these models corresponded to nesting habitat type, nest type, nest component, longevity, fecundity, developmental mode, sexual dimorphism, distributional range size and bill index. However, to evaluate the effect of those presumably important but initially excluded variables (i.e. nest builder sex, mating system and HFI), we repeated the analyses on a reduced dataset that included all predictors without multicollinearity problems (n = 87, 61 species; 'All reduced' and 'Plastic reduced' models). In case of the models with the maximum number of records and 'All' as the response variable (i.e. 'All' models), we ran models for iterations between 1 100 000 and 2 200 000 with 10-20% as burn-in and a sampling interval of 600–1 000, depending on the complexity (i.e. the number of predictors) in the model. We changed the length of chains and the sampling interval as follows: 1 650 000 iterations and 1 000 sampling interval for 'Plastic' models; 330 000–550 000 and 200–300 for 'All reduced' models; 3 300 000–11 000 000 and 2 000–5 000 for 'Plastic reduced' models. These settings allowed us to collect >1 000 posterior samples of chains for estimating the model parameters, for all models, and to maintain the autocorrelation between stored iterations at or below 0.10 [57]. We assessed chain mixing and model convergence by visual inspection of the trace plots after every run. All analyses were performed in R v4.2.2 [58].

3. Results

Our systematic review provided information about ANMs in almost 35 000 nests of 176 bird species and indicated that birds incorporate solid waste materials into their nests on all continents except Antarctica (figure 1b). Out of a total of 855 ANM items identified in 75 scientific papers (table S1), 58.5% were plastic, 19.7% cloth, 8.5% paper, 8.5% were other materials and 4.8% were metal. We identified five subcategories that represented more than 70% of all synthetic materials within the plastic category: string/rope (21.6%), foil/sheet (19.2%), thread (14.0%), hard plastic (11.4%) and bags (6.2%). The most common subcategories of other ANM categories were: straps (44.7% of all cloth items), paper (82.2% of all paper items), wire (24.4% of all metal items) and polyurethane foam (38.4% of all 'Other' items). More detailed information of the relative importance of each subcategory of ANMs can be found in the supplementary material (figures S2–S6).

Our more restrictive comparative analysis included nine predictors and used 'All' as the response variable. Our minimal model indicated a significant association with nest type (dome) and sexual dimorphism (pMCMC = 0.0494 and 0.0459, respectively; table 1a, figure 2). The results of the full model showed a similar pattern (table S2). For our comparative analysis that included 12 independent variables and 'All' as the response variable, we also found nest type (dome) as a significant predictor (pMCMC = 0.016; table 1b) but not sexual dimorphism that was not retained in the minimal model. In contrast, nest component had a pMCMC value of 0.048 and was retained, this being revealed in the full model (table S3, figure 2, figure 3).

The subset of comparative analyses for the plastic subcategory (i.e. 'Plastic') offered partially similar results. The minimal model showed a significant association between the response variable and nest type (dome), nest component (figure S7) and sexual dimorphism (pMCMC = 0.0413, 0.0493 and 0.0013, respectively; table 2a). In addition, nesting habitat (natural) was also highly significant (pMCMC < 0.0001; table 2a). Nesting habitat and sexual dimorphism were also significant predictors in the full model (table S4). The minimal model of the restricted predictors offered completely different results in that nesting type (hole), rather than nest type (dome), was significant (pMCMC = 0.016; table 2b). No predictor was clearly highlighted by the full model in this case (table S5).

4. Discussion

(a) Diversity of anthropogenic nest materials

Our review identified a wide variety of ANMs that are incorporated into birds' nests (table S1) with plastic being the principal category. This finding is not surprising given that plastic is one of the main anthropogenic synthetic substances with a current production reaching 348 million tonnes per year [59] or that global estimates indicate that the majority (79%) of all plastic ever produced persists in the environment to this day [13], and thus is environmentally available. However, not all forms of plastic in the various subcategories identified are equally incorporated into avian nests. Plastic string/rope, foil/sheet and thread were the three most common plastic ANMs that we found reported in nests. To birds, these plastic items may possibly resemble natural nest materials such as vegetation fibres or plant leaves [26,29,31], but how much they resemble plastics to birds has yet to be tested [9]. Cloth was the second most common type of ANM that we identified. Straps and threads were the most commonly reported items of cloth. Again, these and other common objects in nests such as paper, cloth stuffing or even metal wire may also closely resemble natural nest materials to nest-building birds. Testing this possibility is particularly interesting to identify potential ANMs selectivity patterns by birds. Specifically, the potential lack of certain types of natural nest materials in the nest of some species may possibly drive the selection for certain types of ANM. For example, Antczak *et al*. [31] suggested that horse hair which is commonly incorporated into great grey shrike (*Lanius excubitor*) nests on farmland has decreased as the availability of plastic string has increased. However, other items such as hard plastic, pet bottles, polyurethane foam or glass that used as ANMs by several bird species (table S1) seemingly bear little resemblance to natural materials and so it is unlikely that they are incorporated into birds' nests simply because they do not resemble natural nest materials for this species.

From our literature search we discovered that the forms of ANM used in nests varied between marine and terrestrial environments (table S1). Following the AVH, this variation could simply be down to the different abundance of ANMs between the environments. At a broad scale, in marine environments waste pollution often accumulates in aggregations, particularly when composed of floating materials [60] in contrast to terrestrial environments, where pollution is typically dispersed more widely across the landscape [21,61]. In marine environments, a wide range of fishing gear such as rope, string, fishing line, mesh, netting and lobster pot tags [14,16,17,19,36–38,62], and other plastics such as food wrapping, plastic bags, cords and sheets [16,38,63,64–68] were documented in birds' nests. In terrestrial environments that are heavily modified by humans (e.g. urban areas) ANMs included cotton threads, plastic broom fibres, paper, sweet wrappers, cigarette butts, polyethylene, paper towels, wet wipes, synthetic cotton, dental floss and bottle labels [20,23,24,69–71]. Urbanisation is usually associated with solid waste production [33] and it is known to concentrate macroplastics [59], potentially explaining the presence of such objects. Meanwhile, in terrestrial farmland environments, ANMs included agricultural materials such as baler twine, string, wire, nylon sacks [29,72] and other materials such as plastic bags, foil, paper, tape, synthetic fibre and rubber bands were also regularly found [7,15,27,31,73,74]. In freshwater wetlands, ANMs included cardboard, foam rubber, filament, wadding, paper [75] and artificial plants, food packaging, cigarette pack foil and straws [76]. Finally, in relatively unmodified terrestrial habitats such as woodlands surrounded by extensive grassland, ANMs included string, various plastic items and coir [26].

(b) Costs and benefits of anthropogenic materials in nests

There are several costs and benefits to birds of using ANMs (table 3). Some of them are supported by rigorous empirical studies whilst others are merely theoretical suggestions yet to be substantiated by empirical studies. First, ANMs such as plastic string/twine play a role in sexual selection [15,28,30,67]. Empirical support was provided by Sergio *et al*. [28] who showed that black kite pairs that decorated their nests with large quantities of white plastic fledged more offspring and occupied higher quality territories that they were better able to defend compared with conspecifics on nests containing less white plastic. Furthermore, kite pairs in low quality territories removed ANMs that were experimentally placed into their nests, suggesting that such ANM is an honest signal of need [28]. The underlying mechanism determining this behaviour is that the avian nest is an extended phenotype of the builder [42], with decorated nests reliably providing information about the status and/or body condition of the builder [77]. This potential benefit is the main support for the SH. In contrast, cigarette butts do not provide such a signalling benefit in song thrush nests [44]. Igic *et al*. [44) suggested that any such signalling benefit might be communicated through other sensory modalities (e.g. smell) but this seems unlikely given that environmental odours used by birds are typically associated with anti-parasitic or anti-predator functions [78].

A series of observational and experimental studies has found evidence of a clear anti-parasitic function of the cellulose acetate from cigarette butts used by house finches (*Haemorhous mexicanus*) and house sparrows (*Passer domesticus*) as ANMs [23]. Butts from smoked cigarettes retain nicotine and other compounds that may act as arthropod repellents because the abundance of ectoparasites within their nests was negatively related to the amount of cigarette-derived cellulose acetate [23]. This benefit would be associated with an ‘anti-parasitic hypothesis’ that might propose the use of ANM by birds to reduce the parasitic pressure on adults and offspring. A similar idea but involving potentially harmful microbes was suggested by Reynolds *et al*. [9] but such a hypothesis remains to be tested empirically.

Bletter *et al*. [75] suggested that polyester wadding has higher insulative properties than natural materials, and thus helps parents to maintain their offspring at or close to an optimal temperature. Other relatively frequently reported ANMs such as cloth stuffing or polyurethane foam may perform a similar function in supporting the 'thermal hypothesis' proposed by Igic *et al*. [44]. This adaptive function of ANM may be vitally important because offspring experience suboptimal development or mortality above or below the optimal temperature, respectively [2,79]. Again, there are no empirical data to test this thermal hypothesis and so further studies that compare the relative insulative properties of natural and ANMs are urgently needed.

Some authors suggest that ANMs are readily available in the environment and are highly visible, implying that birds collect ANMs such as plastic string/twine because they are easy to find [10,15,31,80]. This is directly related to the AVH that proposes that collecting ANM reduces temporal and energetic costs of adults in searching for and collecting nest materials. Unfortunately, this remains untested and would require manipulative studies to be properly demonstrated. In contrast, other authors suggest that plastic string/twine [67] and synthetic fibre [27] are only used when natural nesting materials are in short supply. Lee *et al*. [38] provided the only experimental evidence to date of black-faced spoonbills preferring natural if available than anthropogenic materials to build their nests.

The last benefit identified in our literature review is the strengthening of the nest structure. Several studies have suggested, but not proven, that plastic string/twine [10,15,31] and artificial plants in the nests of Eurasian coots (*Fulica atra*) on Dutch canals [76] strengthen the structure of nests and thus help to ensure that nests remain intact. According to this 'structural hypothesis', the use of ANMs could provide an important selective advantage to birds nesting in areas prone to frequent storms and high winds, for example, that could compromise the nest structural integrity.

The use of ANMs many also incur costs with perhaps the most well-known being the risk of entanglement or ingestion. Several studies have shown that adults and offspring become entangled in ANM such as plastic string/twine [31,37,75]. For example, osprey (*Pandion haliaetus*) chicks became entangled in 12 of 260 (4.6%) nests [72], a total of 63 adult and juvenile northern gannets became entangled [19]. Eleven of 195 (5.6%) American crow (*Corvus brachyrhynchos*) nestlings became entangled in their nests [29], and there was one record of a rufous-backed thrush (*Turdus rufopalliatus*) nestling becoming fatally entangled [20]. According to a previous study [39], 36% of papers on the topic reported entanglement cases. In papers identified in our literature search case, most (83.2%) studies did not report on it but out of those that did, 78.1% reported entanglement events (n = 32).

Other studies have either suggested [75,81–83] or shown [25] that ANMs such as plastic string/twine are ingested by offspring. Illustratively, Henry *et al*. [73] reported that white stork nests contained an average of six, and a maximum of 27, rubber bands, and 26% of necropsied storks had rubber bands in their digestive tracts which caused fatal gut occlusion in seven instances. Jagiello *et al.* [39] reported that 20% of papers on the topic reported ingestion of ANMs. However, such information is usually absent from papers but of the 12 that do provide data, ANM ingestion is equivocal.

It has also been suggested that ANMs such as synthetic fibres [27] are more colourful and thus, less camouflaged, than natural nest materials, thereby potentially attracting predators to nests. This idea has received empirical support from Møller [15] who found common blackbird nests containing fragments of plastic bags suffered higher levels of nest predation than nests that did not. However, while in some circumstances ANMs may attract predators, in others they may deter them. For example, ANMs could induce neophobia in nest predators in the same way as other nest-associated human-made objects do (e.g. cameras; [84]), an intriguing possibility that has not been tested so far. Furthermore, if ANMs are used in lieu of natural materials but do not have similar properties (e.g. odours, thermal properties), it is possible that a cost of using ANM is that the appropriate material is not used. This is a different cost incurred from ANMs that have properties that are actually harmful to the nesting birds.

Finally, a number of other varied costs of ANMs have been proposed. It has been proposed [64,69,75] that they may cause nests to cool quicker than natural nest materials, creating suboptimal nest microclimates [2]. Hanmer *et al.* [85] found that blue tit nests containing more ANMs held more fleas (Siphonaptera) than those containing less ANMs or only natural materials. Moreover, despite cigarette butts having clear benefits for house finches, they also inflict physiological costs such as erythrocyte genotoxicity on chicks [23]. Plastics or related materials can be toxic or have endocrine-disruptive effects. Such impacts highlight the need for extensive and urgent research addressing the adaptive (or maladaptive) functions of ANM usage by birds.

(c) Interspecific variation in the use of anthropogenic nest materials

Our comparative analyses indicated that sexual dimorphism, nest type and nest component are important species' traits that significantly explain the variation in ANM usage among birds. The results provide interesting and novel information supporting the SH but failing to support the AGH and NLH. In the case of plastics, we found support also for the AVH.

The SH proposes that those species experiencing more intense sexual selection will use ANMs more often based on the assumption that nests can be considered an extended phenotype in birds, potentially providing benefits while avoiding some costs associated with sexual selection [42]. We found that species with larger females used

ANMs more often, an effect that was even stronger in restricted analyses of just plastic items, the most observed ANM. Females are the main nest builders in birds [86], something also observed in our dataset in 93.5% of species (37.4% without male participation). Thus, females would be the ones more likely to use ANMs in a sexual signaling context as they are the ones determining the presence of ANMs in their nests. However, this does not mean that males cannot use ANMs in a similar way, especially since both sexes construct nests in many species [86]; 56.1% of species in our study). Furthermore, we found no association between ANM use and nest builder sex. The SH does not only address sexual selection and, indeed, it was originally proposed in a resource defense context [28]. Therefore, exploring ANM use within other communication frameworks (e.g. interspecific competition, predator-prey interactions) seems granted. Future studies should also consider the role of the different types of ANMs associated with this signaling role. We found a stronger association between the use of plastic and sexual dimorphism. Some ANMs such as plastic string/twine may be stronger signals through elevated visibility and persistence in the environment than others such as paper or cigarette butts. Alternatively, it is possible that sensory biases are involved in the collection of colourful plastic materials with females, and also males, being the target of sensory traps. This may, in turn, bias the collection of colourful ANM towards those resembling the ornaments of their potential partners. This may explain why plastic ANMs are more prevalent in some taxa than others, whereas no such biases exist when plastics are gathered for other purposes.

We also found partial support for the AVH. On the one hand, we found that species nesting in more natural habitats are significantly and negatively associated with ANMs such as plastic items but this was only marginally significant in models including all ANMs. This supports our prediction of lower use of ANMs in species nesting in less polluted habitats where sufficient natural materials may be available for nest building, although this remains untested. On the other hand, we found no significant association with the HFI, another proxy for anthropogenic pressure. These results markedly contrast with those of Jagiello *et al*. [39] who found a significant association in 19 bird species. These contrasting results could be due to different methodological approaches such as the utilization of a slightly different HFI range (2 km in our case *versus* 5 km), our use of phylogenetically controlled analyses or the inclusion of a much larger set of species. The latter is pertinent given that we found a marginally significant effect for this predictor for the models using fewer species and no significant association when considering a larger dataset. Distributional range did not offer significant results either, contrary to our prediction. Solid waste materials are not only increasingly abundant but also widespread and can be found in very remote areas. For example, Lavers and Bond [87] quantified the abundance of anthropogenic debris on the beaches of the uninhabited Henderson Island in the southern Pacific Ocean and found that there was an estimated 672 pieces of debris per m^2 of substrate surveyed. In 2017, there were an estimated 37.7 million items of anthropogenic debris weighing 17.6 tonnes on the island, with as many as 26.8 new items being washed up onto the beaches daily [87]. Furthermore, macroplastics are abundant in remote places such as the Amazon estuary [88] and the Sonoran Desert, where 5.6–35.4 plastic bags and 39.2–62.7 balloon clusters per km^2, respectively, have been reported [89]. Worth to mention is the fact that we found clear support for the AVH with the Plastic model, which could suggest that this hypothesis only applies to this type of ANM potentially explaining contrasting results in previous studies.

Interestingly, we found no support for the AGH despite it being a clear expectation according to previous studies of one or two species [21,28]. We found no association between species' longevity and their use of ANMs. This argues against experience being important for birds using ANMs in nests as was proposed by Reynolds *et al.* [9]. This, of course, relies upon a strong association between age and experience, and the interaction between the two may be problematic in analyses if it is non-linear in some species (e.g. black kites; [28]; white storks; [7]). Our findings suggest that multiple selective forces (e.g. experience, sexual selection) could be acting simultaneously in some species and, therefore, that no single hypothesis can explain ANM use in birds.

Based on our results, we are unable to accept or reject the NLH definitively. Seemingly, contrary to our prediction, bird species living in urban areas do not use ANMs more often. Furthermore, few (10%) of human-made items in avian nests are integrated into the structural part of nests which would also go against the expectations of this hypothesis. However, due to the high percentage (~87%) of records with no specific information, we are uncertain of the patterns of usage of ANMs. Thus, we assume if plastic items can be more easily used with structural functions than other categories such as cloth or paper, this is an intriguing possibility albeit an untested one. In fact, plastic is the only ANM suggested to provide a strengthening benefit for birds' nests [31,76] and the four main plastic subcategories in avian nests could make them optimal as structural materials considering their characteristics such as hardness or length. More specific information on the usage of ANMs by birds is urgently needed to test their functions in nests.

We found that nest type was as an important life-history trait that significantly affected the use of ANMs by birds. For instance, ANMs were seldom found in domed nests, a result that persisted in three of the four minimal models constructed in which it always had a negative association. This implies that perhaps domed nests are structurally constrained if ANMs are used in nests of this type. Nests in holes were also retained as a significant predictor in the species-reduced models of plastic with species nesting in holes preferring to use more plastic items in their nests. Future studies should confirm this as the presence of plastic as an ANM in this nest type seems to depend on the number of species (or predictors) included in the analyses.

Finally, we provide some thoughts about the variation of nesting behaviour of birds. First, life-history traits such as fecundity, developmental mode or mating system do not seem to play an important role in the between-species variation in the use of ANMs. Secondly, that bill index did not feature as a significant predictor in models indicates that there are no mechanical restrictions in the use of ANMs by nesting birds. Species may use ANMs similar in shape and form to those (i.e. natural materials) used in their past, suggesting they are 'pre-adapted' to using ANMs in their nests. However, the fact that our study never provided strong support for any hypothesis may be due to the fact that some ANMs fulfill different roles and this possibility warrants further research attention.

(d) Summary and future research directions

In this study, we present novel information about this increasingly common behavioural innovation implying that birds use ANMs to build their nests. By means of a systematic literature search we have identified the main ANMs used by birds and the species in which this interesting behaviour takes place. We have also provided a summary of the adaptive functions that these ANMs provide to bird species along with their associated costs and benefits. Finally, we have provided the first phylogenetically controlled test of several proposed hypotheses related to ANMs, finding clear support for the SH, mixed evidence for the AVH and no support for the AGH or NLH.

We have found that this nesting behaviour was more widely distributed than was initially expected among birds (figure 2), but we still lack information for some other avian taxa (e.g. Psittaciformes, Piciformes) that are known to manipulate inert (anthropogenic) objects; their inclusion in such analyses will likely improve our understanding significantly of the use of ANMs. Moreover, there is some evidence of non-avian nest-building taxa such as squirrels (Sciuridae) using ANMs in a similar context [90], and so further studies on such taxa may provide important insights of this behaviour too. The geographic scope of studies should expand well beyond western Europe and south-east Australia [91,92]. While we have identified a lack of studies of certain developmental stages of birds (e.g. eggs), we feel that the onus of future studies should be on experimental ones of the adaptive or functional role of a diverse array of ANMs [93] because we currently lack empirical support for many of the costs and benefits detailed in table 3. Furthermore, we need to increase the number of studies exploring the association between ANMs and fitness [21,28] because this is critical to our understanding of this behaviour.

Our final point is to highlight the need for a standardized methodology for studies in this topic, particularly in the quantification of ANMs because some studies have used images of nests [62,94] or nest dissection [21,26,27] to generate ANM data. Even those studies using the latter method do not use a consistent ANM classification and we propose therefore that the Item List from the standardized protocol of the CSIRO Global Leakage Baseline Project

([46]: https://research.csiro.au/marinesolidwaste/resources/) be used by researchers. This protocol is sufficiently robust that it can be used to quantify also ANMs in the vicinity of nests, thereby generating meaningful availability data for environmental ANMs [21]. We hope that this study and its recommendations result in a better understanding of why avian and non-avian taxa use ANMs in their nests.

Ethics. This desk-based study required no ethical approval.

Data accessibility. The data are provided in the electronic supplementary material.

Authors' contributions. Z.J.: conceptualization, data curation, investigation, methodology, validation and writing—original draft; S.J.R.: conceptualization, data curation, investigation, methodology, validation and writing— review and editing; J.N.: conceptualization, data curation, formal analysis, investigation, methodology, validation and writing— review and editing; M.C.M.: conceptualization, data curation, investigation, methodology, validation and writing—original draft; J.D.I-Á.: conceptualization, data curation, investigation, methodology, validation and writing—original draft.

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

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Figure 1. (*a*) Examples of birds' nests containing anthropogenic material. Nests of a (1) common blackbird (*Turdus merula*) containing black plastic string, (2) blue tit (*Cyanistes caeruleus*) containing stuffing materials, (3) white stork (*Ciconia ciconia*) containing various ANMs (e.g. cardboard paper, plastic string and foil) and (4) Caspian gull (*Larus cachinnans*) also containing various ANMs (e.g. plastic, aluminium foil, plastic string). (Photos: [*1*], [*2*] & [*4*] – ZJ, [*3*] – Weronika Baranowska). (*b*) The geographic location of studies identified by our literature search that have quantified the presence of ANMs in birds' nests.

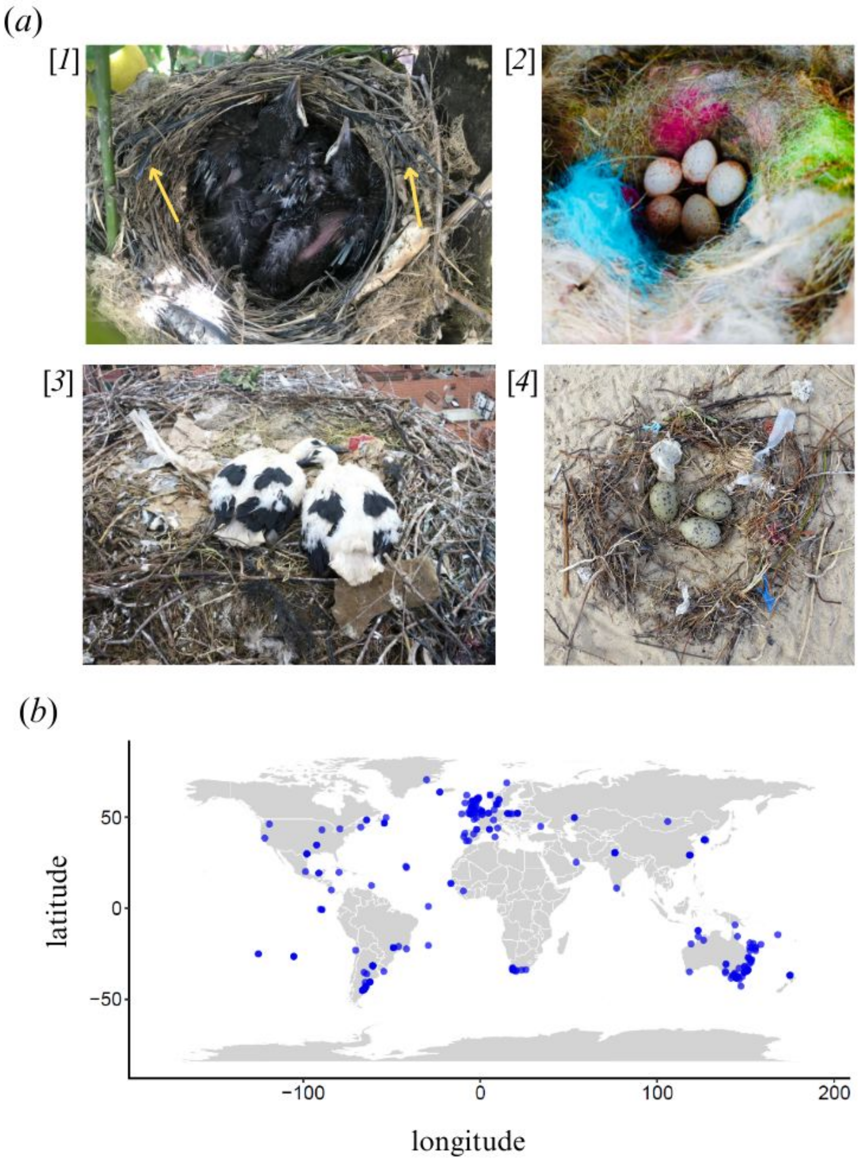

Figure 2. Main results of the phylogenetically corrected comparative analyses. Only predictors included in the minimal models are included in the representation. 'All' and 'Plastic' corresponds to the analyses of all ANMs using nine predictors (in the full model) and 125 bird species (n = 237 records) while 'All reduced' and 'Plastic reduced' refers to the analyses using 12 predictors (in the full model) but 61 bird species (n = 87 records). Solid boxes and lines indicate 5%, 25%, 75% and 95% quantiles of the posterior values per each parameter estimated. (Note: Nest type (hole) was excluded due to substantially larger values, but see Figure S7).

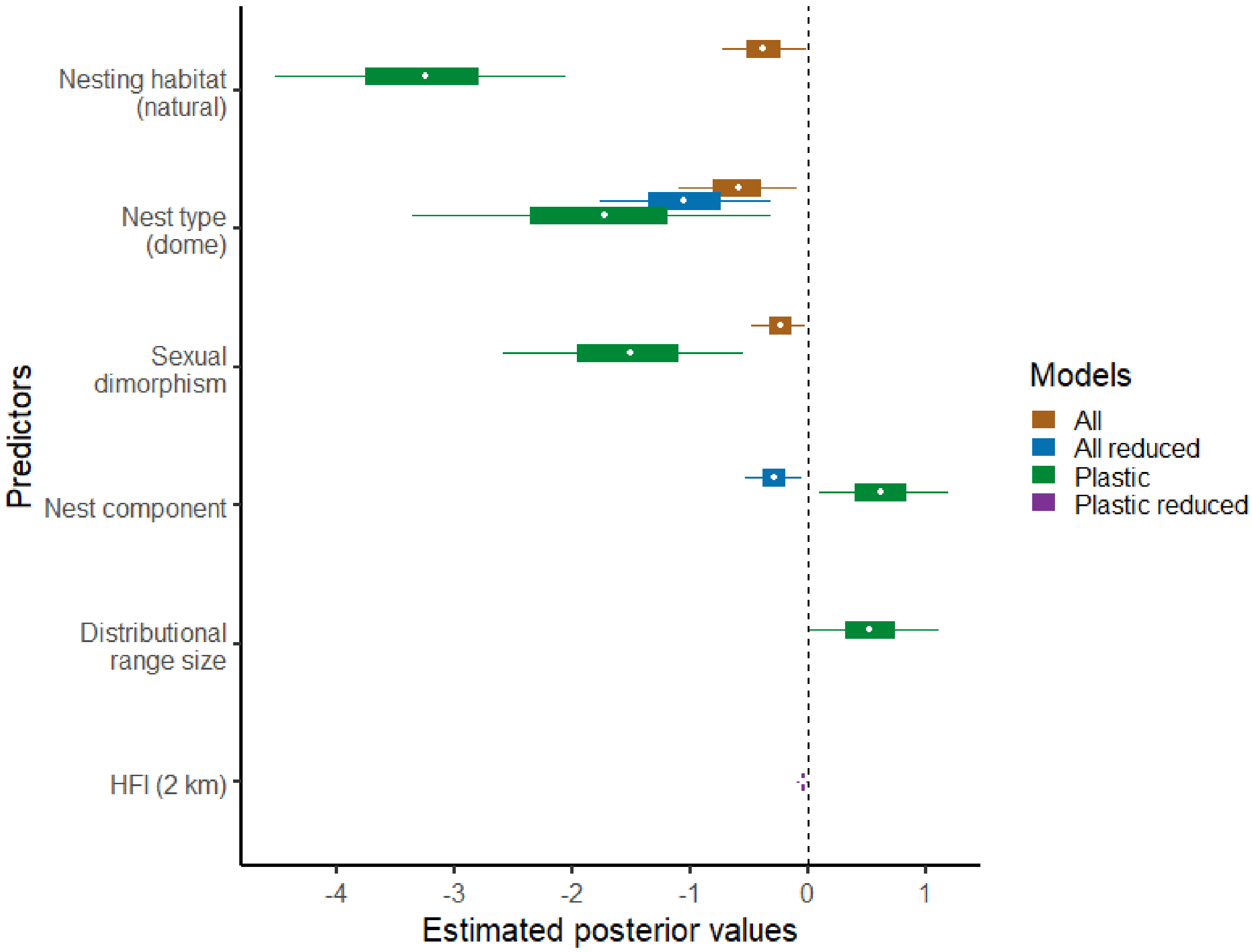

Figure 3. Distribution of ANMs through the avian phylogeny. The figure shows the phylogeny of the bird species used in our comparative analyses and the number of items ('value') incorporated into their nests for all ANMs ('All') and in five categories (plastic, paper, cloth, metal and other).

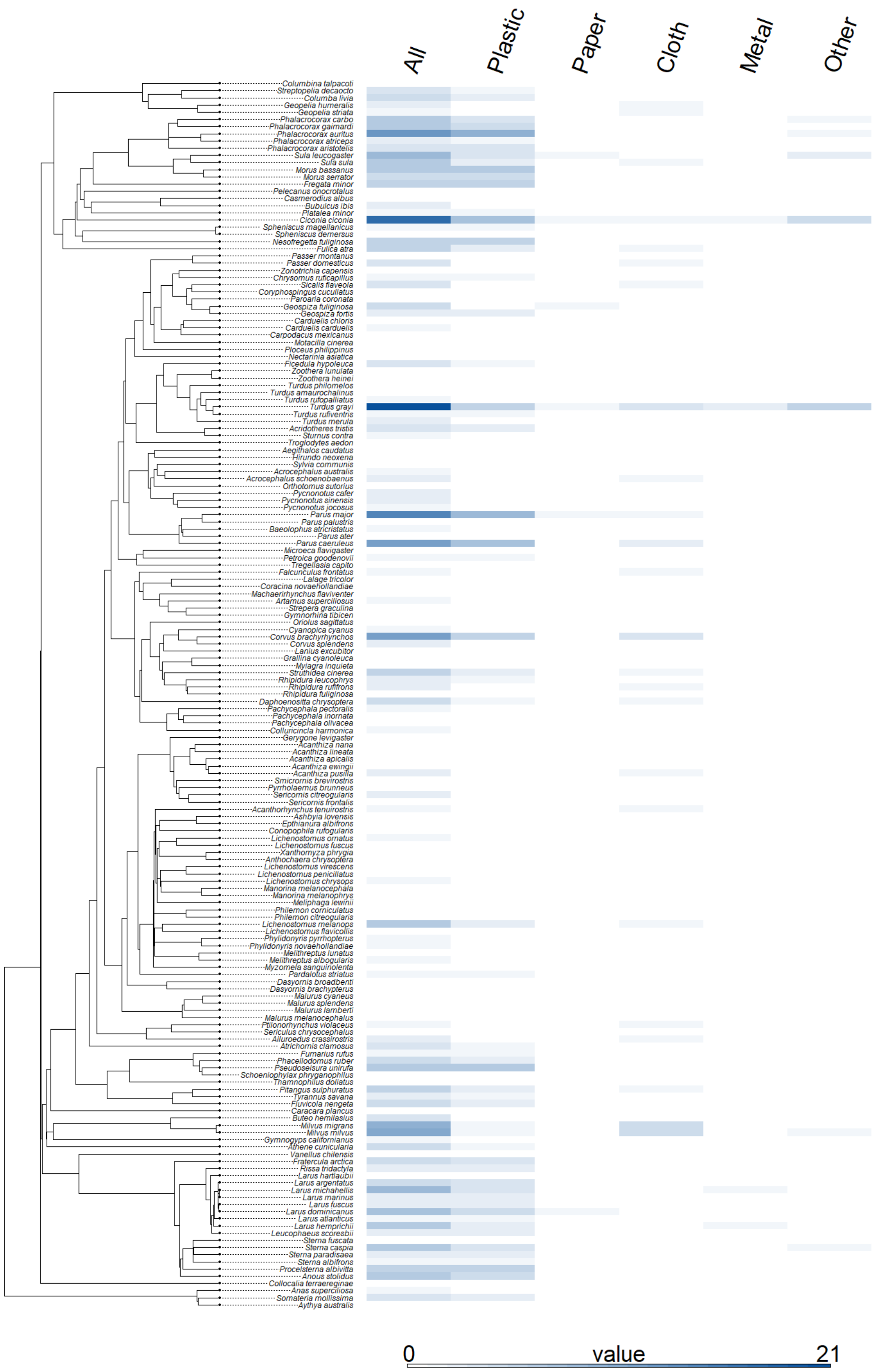

Table 1. Results of the minimal models for the comparative analyses of the number of all categories of ANMs used by birds ('All') for the set of (*a*) nine predictors (n = 125 species), and (*b*) 12 predictors (n = 61 species). Significant predictors are highlighted in italics. Please see tables S1 and S2 for details of the full models. DIC indicates the deviance information criterion.

(a) All (nine predictors minimal model) (n = 237 records)

DIC = 981.618

	posterior mean	lower 95% confidence interval (CI)	upper 95% CI	effective sample	pMCMC
(intercept)	0.977943	0.542353	1.345173	1 700	0.0006
nesting habitat (natural)	-0.376333	-0.796672	0.043225	1 488	0.0835
nest type (dome)	*-0.597395*	*-1.183640*	*-0.004642*	*1 700*	*0.0494*
sexual dimorphism	*-0.239166*	*-0.516337*	*0.014896*	*1 700*	*0.0459*

(b) All (12 predictors minimal model) (n = 87 records)

DIC = 369.832

	posterior mean	lower 95% CI	upper 95% CI	effective sample	pMCMC
(intercept)	2.07787	0.93099	3.23807	1 500	0.0013
nest component	*-0.28996*	*-0.59286*	*-0.01856*	*1 500*	*0.0480*
nest type (dome)	*-1.05610*	*-2.00030*	*-0.22713*	*1 205*	*0.0160*

Table 2. Results of the minimal models for the comparative analyses of the number of plastic items in bird nests ('Plastic') for the set of (*a*) nine predictors (125 species), and (*b*) 12 predictors (61 species). Significant predictors are highlighted in italics. Please see tables S3 and S4 for details of the full models. DIC indicates the deviance information criterion.

(a) Plastic (nine predictors minimal model) (n = 237 records)

DIC = 166.906

	posterior mean	lower 95% confidence interval (CI)	upper 95% CI	effective sample	pMCMC
(intercept)	1.49558	-1.68535	4.86164	1 203	0.35067
nesting habitat (natural)	*-3.26808*	*-4.72449*	*-1.72904*	*1 519*	*0.0007*
nest component	*0.62337*	*0.04480*	*1.32356*	*1 180*	*0.0493*
nest type (dome)	*-1.77934*	*-3.63149*	*-0.01092*	*1 500*	*0.0413*
sexual dimorphism	*-1.54251*	*-2.67966*	*-0.25868*	*1 500*	*0.0013*
distributional range size	0.53443	-0.16584	1.15123	1 349	0.1013

(b) Plastic (12 predictors minimal model) (n = 87 records)

DIC = 52.665

	posterior mean	lower 95% CI	upper 95% CI	effective sample	pMCMC
(intercept)	5.534764	-1.294495	11.671321	2 172	0.0773
HFI	-0.044128	-0.111123	0.005441	1 222	0.0880
nest type (hole)	*8.126308*	*1.287139*	*16.099165*	*1 634*	*0.0160*

Table 3. Costs and benefits of various ANMs in birds' nests, evidence type (E – experimental, O – observational, T – theoretical) and references documenting them.

	nest material	evidence type	references
costs			
altered physiology	cigarette butt	O	Suárez-Rodríguez & Macías, 2014; Suárez-Rodríguez *et al.*, 2017
entanglement	plastic string/twine	O	Blem et al., 2002; Antczak *et al.*, 2010; Votier *et al.*, 2011; Bond *et al.*, 2012; Townsend & Barker, 2014; Carbó-Ramírez *et al.*, 2015; Bletter *et al.*, 2020
increased parasitism	treated cotton and artificial stuffing material	O	Hanmer *et al.*, 2017
ingestion by offspring	plastic string/twine, and rubber bands	O	Bletter *et al.*, 2020; Lato *et al.*, 2021; Henry, 2011
suboptimal nest microclimate	plastic string/twine, and polyester wadding	E	Lopes *et al.*, 2020; Corrales-Moya *et al.*, 2021; Bletter *et al.*, 2020
increased nest predation	synthetic fibres and plastic bags	O	Broughton & Parry, 2019; Møller, 2017
benefits			
amenable nest constituent	plastic string/twine, and synthetic fibre	T	Antczak *et al.*, 2010; Potvin *et al.*, 2021; Henderson *et al.*, 2022; Verlis *et al.*, 2014; Broughton & Parry, 2019
anti-microbial protection	many ANMs	T	Reynolds *et al.*, 2019
improved nest microclimate	polyester wadding	T	Igic *et al.*, 2009; Bletter *et al.*, 2020
predator repulsion	cigarette butts	T	Igic *et al.*, 2009
ectoparasite repulsion	cellulose acetate from cigarette butts	E, O	Suárez-Rodríguez *et al.*, 2013, 2014
sexual signalling	plastic string/twine	E, O	Sergio *et al.*, 2011; Verlis *et al.*, 2014; Zduniak *et al.*, 2021; Henderson *et al.*, 2022; but see Igic *et al.*, 2009
reinforcement of nest	Plastic string/twine, and	T	Antczak *et al.*, 2010; Potvin *et al.*, 2021; Henderson *et al.*, 2022; Hiemstra

structure	artificial plants	*et al*., 2021

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