Science of the Total Environment 838 (2022) 156034

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

The extended avian urban phenotype: anthropogenic solid waste pollution, nest design, and fitness

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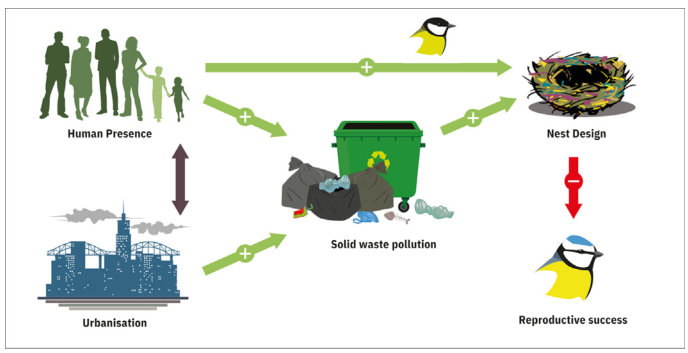
HIGHLIGHTS

- Human presence and urbanisation positively covary with solid waste pollution.
- Urban solid waste pollution covaries with avian nest design and fitness.
- Human presence positively covaries with solid waste in great tit nests.
- The more anthropogenic materials in nests, the less fur and feathers
- Anthropogenic nest materials negatively covary with blue tit breeding success.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Rafael Mateo Soria

Keywords:
Urbanisation
Plastic pollution
Nest
Reproductive success
Human presence
Solid waste

ABSTRACT

Solid waste pollution (garbage discarded by humans, such as plastic, metal, paper) has received increased attention given its importance as a global threat to biodiversity. Recent studies highlight how animals incorporate anthropogenic materials into their life-cycle, for example in avian nest construction. While increasingly monitored in natural areas, the influence of solid waste pollution on wildlife has been seldom explored in the urban habitat. There is limited data on the relationship between anthropogenic solid waste pollution, nest design, and reproductive success in an urban context. We address this knowledge gap (i) by investigating the presence of environmental solid waste pollution in the breeding habitats of great tits *Parus major* and blue tits *Cyanistes caeruleus* reproducing in a gradient of urbanisation, and (ii) by quantifying (ii) the contribution of different anthropogenic materials in their nests. We further examine potential drivers of solid waste pollution by inferring three distinct properties of the urban space: environmental solid waste pollution on the ground, human presence, and the intensity of urbanisation (e.g impervious surfaces) in nestbox vicinity. Finally, (iii) we explore the relationship between anthropogenic nest materials and reproductive success. We found that environmental solid waste pollution was positively associated with human presence and urbanisation intensity. There was also a positive relationship between increased human presence and the amount of anthropogenic materials in great tit nests. Interestingly, in both species, anthropogenic nest materials covaried negatively with nest materials of animal origin (fur and feathers). We suggest that fur and feathers – key insulating materials in nest design – may be scarcer in areas with high levels of human presence, and are consequently replaced with anthropogenic nest materials. Finally, we report a negative relationship between anthropogenic nest materials and blue tit reproductive success, suggesting species-specific vulnerability of urban birds to solid waste pollution.

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http://dx.doi.org/10.1016/j.scitotenv.2022.156034
Received 26 January 2022; Received in revised form 12 May 2022; Accepted 14 May 2022
Available online 18 May 2022

1. Introduction

Humans are waste producers on a massive and global scale; the rate of solid waste production is rapidly increasing, and is estimated to double by 2050 relative to current estimates (Kaza et al., 2018). At least 37% of the current *c.* 2 billion tonnes of waste generated annually ends up in landfills or natural areas, constantly accumulating in the environment (Kaza et al., 2018). Among all anthropogenic materials contributing to waste, plastic emerges as a durable, versatile material that does not biodegrade, but breaks up into smaller pieces instead, dispersing easily in the environment (Ter Halle et al., 2016). Due to these inherent properties, plastic pollution became a global threat to biodiversity (UNEP, 2014), and interacts with other global change drivers such as global warming, landscape use change or biological invasions (Malizia and Monmany-Garzia, 2019). In this context, while a growing number of studies investigated the impact of plastic pollution on marine ecosystems, little is known about the effects of plastic pollution inland, where it is mainly produced (Jâms et al., 2020; MacLeod et al., 2021). Additionally, previous studies have largely focused on microplastics, leaving an important knowledge gap in our understanding of the effects of macroplastics on the environment (Malizia and Monmany-Garzia, 2019).

1.1. Anthropocene: plastic pollution & urbanisation effects on wildlife

Several studies have highlighted the effects of solid waste pollution on free-living organisms, for example by altering their behaviour and physiology (Suarez-Rodriguez et al., 2012). Solid waste pollution, and specifically plastic pollution, has been shown to increase individual mortality due to ingestion, entanglement or entrapment (Gall and Thompson, 2015; Santos et al., 2021). Birds, one of the most affected groups globally (Gall and Thompson, 2015; Wilcox et al., 2015), are known to incorporate anthropogenic materials such as plastic strings or plastic foil pieces into their nests (Jagiello et al., 2019). Plastic strings can cause entanglement of growing chicks, leading to increased mortality rates at this developmental stage (Townsend and Barker, 2014). Other anthropogenic materials used in nest building, such as cigarette butts, can cause genotoxicity in nestlings blood cells, presumably decreasing nestling survival due to their toxicity (Suárez-Rodríguez and Macías Garcia, 2014). However, knowledge of the temporal and spatial variability of anthropogenic materials inclusion into nests is very limited, as is information on the impact of such materials on nest design and avian fitness (Jagiello et al., 2019; Reynolds et al., 2019; Tavares et al., 2016; Antczak et al., 2010).

Nests are the cornerstone of avian reproduction – by providing a secure place for the development of offspring, and by maintaining stable thermal and humidity conditions (reviewed in Deeming and Reynolds, 2016). Nests are also considered as an extended phenotype, defined as non-bodily characteristics of the individual who constructs it (Schaedelin and Taborsky, 2009). Extended phenotypes are often expected to play a key role in sexual signaling, by carrying information on individual fitness and reproductive investment (Järvinen and Brommer, 2020; Schaedelin and Taborsky, 2009) in both natural and human-modified environments (Sergio et al., 2011). It is thus suprising that studies concerning the effect of solid waste pollution on nest building, behaviour and fitness has been seldom explored, particularly in an urban context (Reynolds et al., 2019).

Urban areas are considered key producers of environmental solid waste pollution (Forman, 2014). Radical landscape transformation is required to create cities, therefore urban ecosystems also constitute a major global threat to biodiversity (McKinney, 2002; Grimm et al., 2008). Many studies have readily described urban-induced behavioural, physiological, ecological and evolutionary effects on wildlife (e.g Forman, 2014; Szulkin et al., 2020). However, research to date on the biological impact of urban pollution has largely focused on atmospheric pollution (i.e. gases, light and noise) rather than on solid waste (e.g. Isaksson, 2010; Halfwerk et al., 2011; Dominoni et al., 2013). Surprisingly, few studies have quantified the impact of solid waste pollution across the urban lanscape. Rare exceptions are the work of Radhamany et al. (2016) and Wang et al. (2009), who report a higher use of anthropogenic materials in nest construction by house sparrows *Passer domesticus* and Chinese bulbuls *Pycnonotus sinensis* with increasing urbanisation in Asia. These findings, in addition to the rapid expansion of urban areas worldwide (Seto et al., 2012) and the potential negative effects of solid waste pollution on avian reproduction (e.g. Suárez-Rodríguez and Macías Garcia, 2014), highlight the urgent need of assessing the relationship between cities and the use of anthropogenic materials in nest building and design (Reynolds et al., 2019).

1.2. Why do birds incorporate anthropogenic materials in their nests?

The first reported observation of anthropogenic materials recorded in avian nests dates back to 1933, when Warren (1933) recorded metal wire in a pied crow *Corvus scapulatus* nest. Since then, the number of such observations has considerably increased, reflecting the pervasive nature of human activities at a global scale (Jagiello et al., 2019). Three main (and non-exclusive) hypotheses have been proposed to explain the incorporation of anthropogenic materials into avian nests: i) *availability*, ii) *age* and iii) *adaptive/functional* hypothesis (reviewed in Reynolds et al., 2019).

The *availability* hypothesis predicts an increased amount of anthropogenic material in nests as the result of human activities, (e.g. transformation of land, alterations of ecosystems) and a consequent reduction of natural materials such as plants, animal hair or feathers originally used in nest construction (Antczak et al., 2010; Lee et al., 2015). It implies that in more polluted environments, birds are most likely to use anthropogenic materials to build their nests, as these are more accessible and ubiquitous than natural materials (Lee et al., 2015; Radhamany et al., 2016). To properly test this hypothesis, it is necessary to measure anthropogenic materials both in the nest and in the surrounding environment at the time of nest construction.

The *age* hypothesis refers to an association between the use of anthropogenic materials with the age of breeding individuals, and assume a causal relationship between age and individual experience (Sergio et al., 2011). Previous studies conducted in two long-lived species, the black kite *Milvus migrans* and the white stork *Ciconia ciconia*, reported that older and more experienced individuals are more likely to incorporate anthropogenic materials into their nests (Sergio et al., 2011; Jagiello et al., 2018). Anthropogenic nest materials in those species were likely to serve as an extended phenotype and sexual signal expressing builder quality (Sergio et al., 2011; Jagiello et al., 2018).

The third, *adaptive/functional* hypothesis, links individual behaviour - the incorporation of anthropogenic materials in nest building – to possible associated reproductive benefits and, as such, can also be considered as an extended phenotype (Sergio et al., 2011): for example, cigarette butts may act as ectoparasite-repellent (Suarez-Rodriguez et al., 2012), durable plastic strings may serve to reinforce the structure of the nest (Antczak et al., 2010), and anthropogenic materials may modify nest insulation properties (Reynolds et al., 2019; Corrales-Moya et al., 2021). However, studies demonstrating clear links between individual behaviour in nest building (e.g. the inclusion of anthropogenic materials) and individual fitness are scarce to date (Reynolds et al., 2019). Suárez-Rodríguez and Macías García 2017 showed that anthropogenic nest materials (cigarette butts) act beneficially on the fledging success of House finches (*Carpodacus mexicanus*), but it is also possible that the cost of such exposure (due to toxicity), will only appear in post-fledgling life. Overall, the adaptive potential of the inclusion of anthropogenic nest materials, viewed as a trait in the extended phenotype framework (Sergio et al., 2011), remains poorly understood.

1.3. Study aims

We here studied the association between environmental solid waste pollution, avian nest design and fitness. We specifically focused on two urban adapters – great tits *Parus major* and blue tits *Cyanistes caeruleus* - breeding in a gradient of urbanisation in one of the largest European cities (Warsaw, Poland). First, we examined factors associated with urban environmental solid waste pollution on the ground and in nestbox vicinity. Second, we investigated mechanisms underlying the use of anthropogenic materials in nest design. We specifically tested hypotheses focusing on (1) solid waste availability, (2) parental age, and (3) the adaptive role of solid waste in terms of reproductive success.

2. Methods

2.1. Study sites

Data on environmental solid waste pollution - inferred on the ground and from avian nests - was collected in 2020 during the breeding season of great tits and blue tits (March–June) in the capital city of Warsaw, Poland, and its surroundings. We used eight environmentally heterogeneous study sites arranged in a gradient of urbanisation starting in forested areas outside of the city and ending in the city center (Fig. 1). Specifically, two study sites corresponded to city outskirts (Fig. 1A and B), while the remaining six sites offered different intensities of urbanisation within Warsaw city borders (Fig. 1C-H). The study sites constitute a mixture of habitat patches (suburban village, natural forest, urban parks, residential areas, office areas) representative of the urban mosaic (Forman, 2014). A brief description of each study site is provided below. More details can also be found in earlier studies (Corsini et al., 2019; Szulkin et al., 2020).

2.1.1. Suburban village (number of nestboxes (N) = 47)

Palmiry (20°46′48.9748″E - 52°22′11.3382″N) is a suburban village with *c.* 370 inhabitants: the area is mainly characterized by residential homes with gardens interconnected by tree-lined avenues. A large commercial centre located close to a highway and two small stores are also present in the area.

2.1.2. Natural forest (N = 110)

Kampinos National Park (20°47′14.3867″E - 52°21′22.5409″N) is a large oak-pine forest located in the north–west outskirts of Warsaw. The area is characterized by a mix of forested sand dunes and swamps.

2.1.3. Urban forest (N = 65)

Las Bielanski Natural Reserve (20°57′33.3″E - 52°17′38.2842″N) is the only remnant of the Mazovia Primeval Forest. This deciduous forest is mainly characterized by the presence of oaks (*Quercus* spp.), hornbeams (*Carpinus* spp.) and maples (*Acer spp*). This study site stands as an island of wilderness in the city: with walking paths and resting areas, it also attracts visitors all year around.

2.1.4. Residential area II (N = 52)

Osiedle Olszyna neighbourhood (20°57′39.37097″E - 52°16′23.71883″N) is a block of flats intermixed with green areas, but also schools, groceries and recreational facilities for families. It is located in close proximity to the urban woodland "Las Olszyna" (Site E).

2.1.5. Urban woodland (N = 21)

Las Olszyna (20°57′33.93652″E - 52°16′10.55093″N) is a green area composed of a deciduous, wet alder forest and an adjacent open-space playground.

2.1.6. Office area (N = 28)

The "Ochota" Campus (20°59′8.85224″E - 52°12′43.77676″N) is the University of Warsaw science campus, largely designated for students and university researchers. The area is composed of office buildings, laboratories, dormitories and canteens for students.

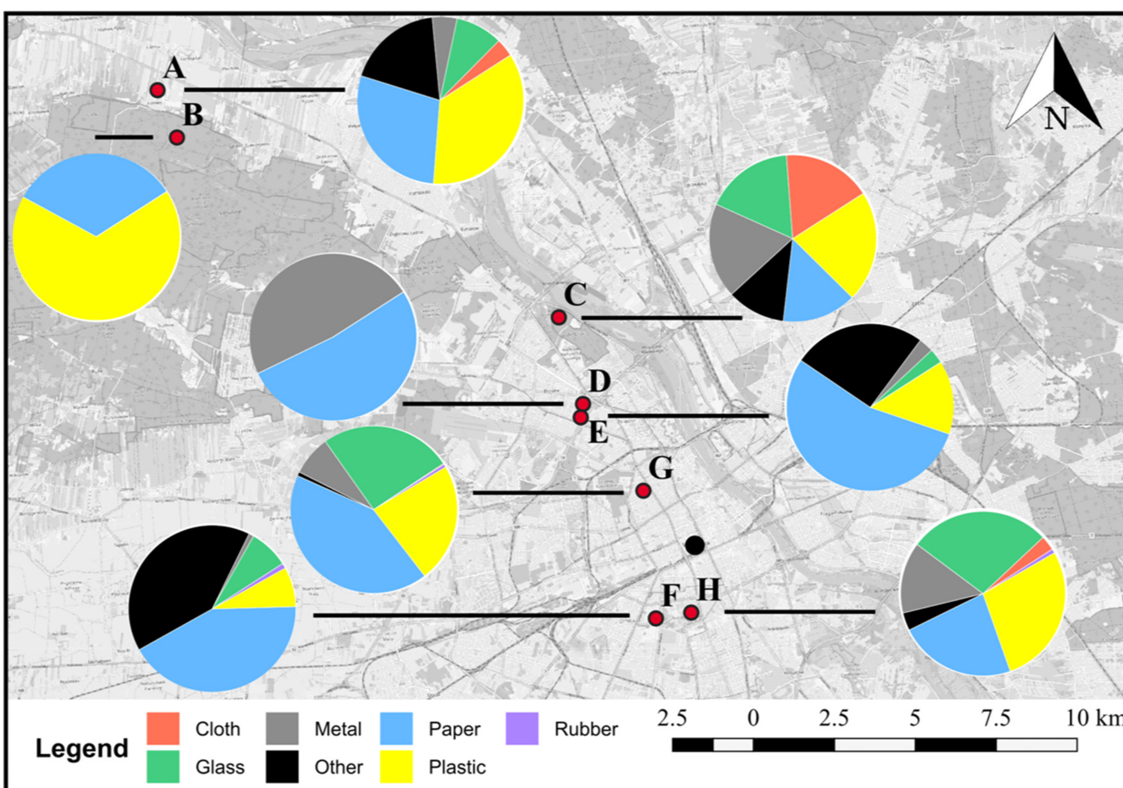

Fig. 1. Study sites and environmental solid waste categories (Transect Data). Study site locations in Warsaw (Poland). Red dots correspond to study site locations, which include: a suburban village (A), a natural forest (B), an urban forest (C), residential areas II (D) and I (G), an urban woodland (E), an office area (F), an urban park (H). The black dot stands for Warsaw city centre. Each piechart shows solid waste categories within each study site (in %). While study sites vary in terms of solid waste composition (as reported on the figure), the amount of solid waste items also varied between study sites; details of this variation are reported in Tables S5.

2.1.7. Residential area I ($N = 46$)

The "Muranow" district (20°59′5.74332″E - 52°14′52.17925″N) is a residential area, similar in structure and use to Residential area II (Site D).

2.1.8. Urban Park ($N = 105$)

Pole Mokotowskie (21°0′6.98321″E - 52°12′46.66874″N) is a large urban park. It includes a combination of habitat patches such as meadows, tree-covered areas and recreational structures (i.e. playgrounds, and numerous sport facilities). It constitutes a centrally-located recreational area for urban dwellers.

2.2. Environmental solid waste pollution survey

To estimate environmental solid waste pollution in the vicinity of avian nestboxes, we used the standardised protocol of the CSIRO Global Leakage Baseline Project, specifically applying the protocol section designed for inland sites (Schuyler et al., 2018; access: https://research.csiro.au/marinesolid waste/resources/). Briefly, this protocol establishes three random, 12.5 m long transects for each sampling location (here – an avian nestbox). To adapt the protocol to our study, we established transects within a radius area of 25 m from a nestbox as its central point. This distance of 25 m around the nestbox is well within the typical territory size of *c.* 1 ha (territory of 100 × 100 m) for these species (Krebs, 1971; Wilkin et al., 2006). Nestboxes in our study area were spaced 50 m from each other, thus avoiding the overlap of transects corresponding to different nestboxes. As soon as nest building started in a particular nestbox, we located and categorised all solid waste items found along each of the three transects attributed to a given nestbox by following protocol guidelines (Schuyler et al., 2018). The main categories of anthropogenic materials detected in the environment included paper, plastic, glass, metal, cloth, rubber and "other". Data from these ground transects, collected for every nestbox where active nest building was taking place, were further used as proxy for environmental solid waste pollution birds were exposed to during the nest building stage.

2.3. Life history data

The eight study sites monitored in this study are home to 474 nestboxes specifically designed for great tit and blue tit breeding (Schwegler woodcrete nestboxes; type 1b, with a 32 mm entrance hole). Starting from the end of March 2020, all nestboxes were checked weekly to identify those occupied by tits, and to record the following life-history traits: egg laying date (1st of April = 1), clutch size and hatching date. Only first broods – defined as broods that started no later than 30 days after the very first brood in a given site – were included in the analyses (Van Balen, 1973). When nestlings were 10 days old, adults were trapped in the nestbox whilst feeding young. Both adults and nestlings were ringed with an alphanumeric metal ring, and basic biometrics were taken. Adults were also aged based on their wing plumage, which allowed to distinguish first-year breeders from older birds (second-year breeders or older). Only female age was further considered in the analyses as in both species, females are the sex that builds the nests (Mainwaring, 2017). All chicks were ringed 15 days after hatching. Finally, individual fledging success was assessed by visiting all active nestboxes *c.* 25 days after hatching to record the number of birds that successfully left the nestbox.

2.4. Nest collection and dissection

We collected 100 great tit and blue tit nests (43 and 57 nests, respectively) once they became inactive, independently on whether they were successful ($N = 76$; at least one offspring fledged) or unsuccessful ($N = 24$; at least one egg was laid but no chick fledged). Successful nests were collected up to 5 days after the fledglings left the nestbox. We excluded predated nests from our analyses as predators often destroy and/or remove part of the nest (Z.J., pers. obs.), thereby preventing the correct quantification of nest materials. Tit nests were gently removed from nestboxes and stored in cardboard boxes at ambient temperature in the field. Within the next 72 h, nests were transported to the University of Warsaw, where they were stored at −80 °C for at least 24 h to halt the process of nest material biodegradation (Mainwaring et al., 2014).

Once in the lab and after freezing, we measured nest total weight using an electronic scale to the nearest 0.0005 g. We further dissected nests following Mainwaring et al., 2014. Natural nest materials categories were based on Hanmer et al., 2017, but these were adjusted to reflect the content found in great tit and blue tit nests (Table S1). Soft elements of animal origin – these included fur, human hair and feathers - were combined into the *animal origin* category; these materials were mostly limited to the lining part of the nest cup (Z.J. pers. obs.). *Moss*, *grass* and *other (natural elements)* categories followed, the latter including bark, needles and twigs. Finally, we also introduced the *compos*t category, which included all plant-based elements that were impossible to assign elsewhere due to decomposition. Anthropogenic nest materials were categorised with the same protocol that was used for ground transect quantification (Schuyler et al., 2018, Table S2), with one adjustment: in ground transects, the sampling unit for recording environmental solid waste pollution were counts (e.g. the number of items in each anthropogenic solid waste category recorded along a transect). This approach was not feasible while quantifying the contribution of anthropogenic materials in nest design: indeed, tits tear solid waste items into many small pieces (Z.J., pers. obs.). Therefore, the amount of anthropogenic nest materials was weighed rather than counted (Fig. S1).

2.5. Human presence and urbanisation intensity

We used a readily computed, repeatable estimate of human presence around each nestbox following methodology detailed in Corsini et al., 2019. Briefly, the human presence index reports the number of humans and dogs detected in a 15 m radius around each nestbox during a 30 s long count (Corsini et al., 2019), averaged over 20 counts performed during the day and across the breeding season. The total observation time per nestbox during the breeding season was 10 min. The estimate of human presence was found to be repeatable over time (Corsini et al., 2019), and humans - recorded as pedestrians and bikers - contributed 93% to the dog and human presence index in this dataset (Table S3).

Urbanisation intensity was computed as the percentage of Impervious Surface Area (ISA) in a 100 m radius around each nestbox as described in Szulkin et al. (2020). Briefly, ISA was calculated in QGIS using a 20 m pixel resolution map of ISA processed via satellite imagery from 2015 (Copernicus Land Monitoring Services, https://land.copernicus.eu/sitemap). This index includes all types of built-up areas, such as infrastructural networks (roads), parking lots and buildings.

2.6. Weather information

Temperature data was included in all null models because nest design in tits was readily found to be associated with local temperature in the timeframe preceding clutch initiation (i.e., lay date, see Deeming et al., 2012). Since rainfall is a strong determinant of breeding success in cavity-nesting birds (Radford and Du Plessis, 2003), it was also included in all null models. 2020 weather data was obtained from the Polish Institute of Meteorology and Water Management (IMGW-PIB). Daily temperature and rainfall were averaged from two stations: Warsaw Okęcie and Legionowo, referring respectively to sites situated within (sites C—H) and outside (sites A&B) Warsaw city borders, to provide fine-scale data on climatic conditions in urban and non-urban sites. Temperature and rainfall were further averaged for each nest for a seven-day period prior to - and including - laying date, following Deeming et al. (2012).

2.7. Statistical analyses

All analyses were performed with the opensource R computing environment (version 4.0.2). All plots were visualised using the R package *ggplot2* (v. 3.1.0.) (Wickham, 2011) and further assembled with the open source

Inkscape software (v.1.0.2) (https://inkscape.org; Oualline and Oualline, 2018). Analyses were performed in great tits and blue tits separately, as (i) these two species may respond to urbanisation differently in terms of anthropogenic nest materials (Hanmer et al., 2017) and (ii) nest structural characteristics are also known to be species-specific (Mainwaring, 2017).

Statistical analyses were performed in a five-step process based on two different datasets: (1) Transect Data (abbreviated as "TD", $N = 100$ sampling locations (nestboxes), covering 300 transects of environmental solid waste pollution from the ground), (2) Nest Data, which includes species-specific data on nest components resulting from nest dissection (abbreviated as "ND" N = 100 nests, 43 of which are great tit nests, and 57 blue tit nests).

2.7.1. Environmental solid waste pollution in a gradient of urbanisation (TD)

For each nestbox, 3 ground transects were surveyed for environmental solid waste pollution. Information on environmental solid waste pollution was collected along 300 ground transects, corresponding to 100 sampling locations surrounding nestboxes. Data from each of the 3 transects per nestbox were summed, and further analyses were run at the nestbox level. Variation in environmental solid waste pollution driven by urbanisation was inferred at two levels – both in terms of (i) the total amount of environmental solid waste pollution and (ii) environmental solid waste pollution composition, partitioned into solid waste type categories (see Section 2.4). Each sampling location (e.g. each nestbox) was defined as located either below or above the median value of (i) human presence and (ii) Impervious Surface Area (ISA) for the entire transect dataset, thereby generating two contrasted levels for each variable (low/high human presence, low/high ISA, respectively). Changes in environmental solid waste composition in low/high human presence or ISA were tested using Chi-square tests of independence (χ^2).

To illustrate the urban environmental differences occurring in low/high environments, we report that for great tits, the average (± SD) number of humans around each nestbox in 30s-long counts were 0.06 (± 0.12) and 1.60 (± 0.99) humans for low and high human presence areas, respectively. Values were equivalent for blue tits, whose nests surrounded by low and high human presence were 0.19 (± 0.19) and 2.15 (± 1.82) humans, respectively. Great tits breeding in low and high ISA environments were surrounded by an average (± SD) of 3.6% (± 3.17) and 21.1% (± 9.62) ISA respectively. Similarly, blue tit nests in this study were characterised by an average of 2.7% (± 2.27) and 17.9% (± 10.06) in low and high ISA environments, respectively (see Summary statistics in Table S4).

2.7.2. Interspecific variation in nest design (ND)

We run a multivariate analysis of variance (MANOVA) to test for differences in great tit and blue tit nest components (modelled in terms of weight (grams)), and a principal component analysis (PCA) using *prcomp* (https://stat.ethz.ch/R-manual/R-devel/library/stats/html/prcomp.html) in R and visualized by *ggord* (Marcus, 2017) to analyse variation within and between nest components in the two target species. Explanatory variables in MANOVA included the weights of: anthropogenic materials, compost, dry grass, feather, fur, moss and other natural materials. Prior to PCA, the weights of all categories of nest components were mean-centered using the function *scale (where* x_i*-*x_{mean} */sd)* in R.

2.7.3. Association between environmental solid waste pollution, human presence, and urbanisation intensity on the weight and proportion of anthropogenic materials in the nest (ND)

Contrasted levels of environmental solid waste pollution, human presence or urbanisation (ISA) were defined as below or above the median of the variable of interest, calculated for each species separately. We first assessed whether these contrasted levels of solid waste pollution, human presence and urbanisation influenced species-specific variation in nest composition using *t*-tests.

We further investigated in detail the extent to which species-specific environmental solid waste (see below), human presence and urbanisation (ISA) influenced the distribution of anthropogenic materials in the nest. For these analyses, we only included those categories of anthropogenic solid waste that were found both in the nests and in the environment (based on transect data). Indeed, not all solid waste items found in the environment were used by great tits or blue tits during nest construction. Before running such models, we generated a new variable reporting environmental solid waste found on the ground, termed "species-specific environmental solid waste", which only includes solid waste items found in species-specific nests (for precise information about species-specific solid waste items, see Supplementary information, Table S2).

We further examined variation in (A) the proportion of anthropogenic materials in the nest, fitted as the ratio of anthropogenic materials relative to nest total weight (in grams), and (B) the total weight of anthropogenic materials in the nest. We tested whether this ratio varies depending on (i) the number of environmental solid waste items found in the surroundings of nestboxes based on transect data, but also (ii) human presence and (iii) urbanisation intensity. Models were tested with Generalised Linear Mixed Effects models (GLMMs, function *glmmTMB* in the R package *glmmTMB,* Brooks et al., 2017) in a model averaging framework. We also assessed the covariation between the amount of anthropogenic materials in the nests (fitted as either a proportion relative to total nest weight or as the total weight of anthropogenic materials in the nest) and the following explanatory variables: species-specific environmental solid waste (fitted as the number of solid waste items identified on transects), human presence, ISA (urbanisation intensity proxy), but also the proportion/weight of components of animal origin (specifically feather and fur, as only these materials, together with anthropogenic nest materials, line the nest cup), as well as temperature and rainfall. This was modelled in a linear mixed model framework using the *lmer* function in the R package *lme4* (Bates et al., 2015). We used a *Z*-score function to standardise the explanatory variables. The proportion/weight of anthropogenic nest materials were fitted as response variables after applying a linear beta transformation (Smithson and Verkuilen, 2006). Study site was included as a random effect to control for the non-independence of broods belonging to the same study location (8 categories). As variance inflation factors (VIF) for all explanatory variables here included were below 2, model structures were not subjected to multicollinearity issues (Zuur et al., 2009). A set of models including all possible combinations of fixed effects were subsequently generated from the global model detailed above (R package *MuMIn* v. 1.43.15, see Bartoń, 2018). Models were classified according to the Akaike's information criterion (AIC_c) to identify those with the best fit (Burnham and Anderson, 2004), and model-averaged coefficients for a subset of models ($\Delta AIC_c < 2$) were further obtained. Because some Akaike weights of best models were below 0.9 and high model selection uncertainty existed, we applied full model averaging (Symonds and Moussalli, 2011). Finally, we extracted upper and lower bounds of 95% confidence intervals (CI) for each variable kept in the best fitting model.

2.7.4. Effect of female age on the presence/absence of anthropogenic nest materials in tit nests (ND)

We carried out additional analyses to test whether there is a relationship between female age and the presence of anthropogenic materials in tit nests. These analyses were performed on a reduced dataset since some nests failed before adults could be caught, and a few age records were missing for some females caught at the nest (thus, $N_{\text{great tits}} = 33$; $N_{\text{blue tits}} = 52$). We used a similar procedure for model building as described in section 2.7.3, but with an additional fixed factor: female age, coded as first year bird vs adult breeder (2 years or older).

2.7.5. Anthropogenic nest materials and reproductive success. (ND)

In a final analytical step, we inferred the relationship between anthropogenic nest materials in avian nest design (e.g. the extended phenotype) and reproductive success (e.g. avian fitness). Fitness was here defined in terms of reproductive success assessed at two life-history stages of the offspring, and measured in terms of number of hatchlings (e.g. the number of chicks that hatched in the brood) and in terms of number of fledged birds (e.g. the number of chicks that successfully fledged from the nestbox). We used Linear Mixed Effects models in a model averaging framework as described above. Analyses were performed at a species level, on nests where at least one hatchling hatched. The total number of hatchlings per breeding event (e.g. the number of chicks that hatched in the nest) was fitted as Gaussian-distributed response variable, while the following parameters were fitted as fixed predictors in the models: species-specific environmental solid waste, proportion of anthropogenic nest materials, human presence, ISA, temperature and rainfall. Variance inflation factors (VIF) for all explanatory variables here included were below 2, so model structure was not affected by multicollinearity issues. The categorical variable "Study site" was fitted as random effect to control for non-independence of nests sampled within the same area and in order to control for site heterogeneity. We further built an equivalent model with an analogous structure, but with the number of fledged birds fitted as response variable (using Gaussian residuals). For significant effects, we calculated and visualized predicted marginal effects quantifying effect sizes of the percentage of anthropogenic nest materials on the number of hatchlings and fledglings using the *ggeffects* package (Lüdecke, 2018).

3. Results

3.1. Variation in ground solid waste pollution across the urban mosaic (TD)

We characterized 300 transects, located within a 25 m buffer zone from 100 nestboxes (3 transects/nestbox) in terms of solid waste pollution on the ground (Fig. 1 and Table S5). A total of 2317 solid waste items were recorded in the study system. The majority of solid waste were identified as *paper* (30.6%, $N = 709$), followed by *plastic* (25.5%), *glass* (21.4%,), *cloth* (2.46%) and *rubber* (0.56%) (see also Fig. 2).

Residential Area I (site G) was the urban area with the highest number of solid waste items detected (Table S5), with *paper* and *plastic* solid waste emerging as dominant categories (Fig. 1). On the opposite end of the pollution spectrum, the lowest incidence of solid waste pollution was found in the Natural forest (site B) with *c.* hundred-fold lower number of solid waste items compared with Residential Area I (Table S5).

When splitting the sampling locations (nestboxes) into two equal groups reflecting high and low levels of human presence and urbanisation ($N = 50$ nestboxes for high and N = 50 nestboxes for low levels), Chi-squared tests of independence (χ^2) revealed significant differences between certain solid waste categories found in the environment (Fig. 2, Table S6). Specifically, in areas characterized by higher levels of human presence, the number of solid waste attributed to *paper*, *glass*, *metal* and *other* categories were significantly higher than in areas with lower levels of human presence ($p < 0.005$, Fig. 2a, Table S6). When looking at contrasted levels of urbanisation related to impervious surfaces (ISA), we recorded a significantly higher number of solid waste items in high-ISA environments for *paper*, *glass* and *metal*, (p < 0.005, Fig. 2b, Table S6), and a significantly lower number of *cloth* items in high-ISA environment (p < 0.005, Fig. 2b, Table S6).

3.2. Interspecific variation in nest design (ND)

A multivariate analysis of variance (MANOVA) revealed clearcut, significant differences in terms of nest composition between species ($F_{7,95} = 10.871$, Pillai = 0.44, p < 0.005), as visualised on Fig. 3. The weight of moss, dry grass, feather and compost were significantly higher in blue tit nests than in great tit nests (Table S7). The amount of fur (in grams) was significantly higher in great tit nests relative to blue tit nests (Table S7). Other nest materials (both natural and anthropogenic) did not differ between species. These results were visualised in a principal component analysis (Fig. 3): the first three principal component axes (PC) explained 29.3%, 20.4% and 15.23% of the total variance, respectively, and contributed to a total variance of 64.9% in nest components (Fig. 3). Nest weight components such as moss, dry grass and feathers were negatively correlated with PC1, and feather and other natural materials correlated positively with PC2. Compost, fur and other natural materials positively correlated with PC2, while the weight of anthropogenic materials correlated negatively with PC2 (Fig. 3a). PC3 was related positively to the weight of anthropogenic materials in the nest, and negatively with moss weight (Fig. 3b).

3.3. Drivers of urban nest design variation

3.3.1. Species-specific nest-composition in the context of environmental solid waste pollution, contrasted levels of human presence and urbanisation

3.3.1.1. Great tit. There was a *c.* 3-fold increase in anthropogenic materials in great tit nests from nestboxes surrounded by high levels of

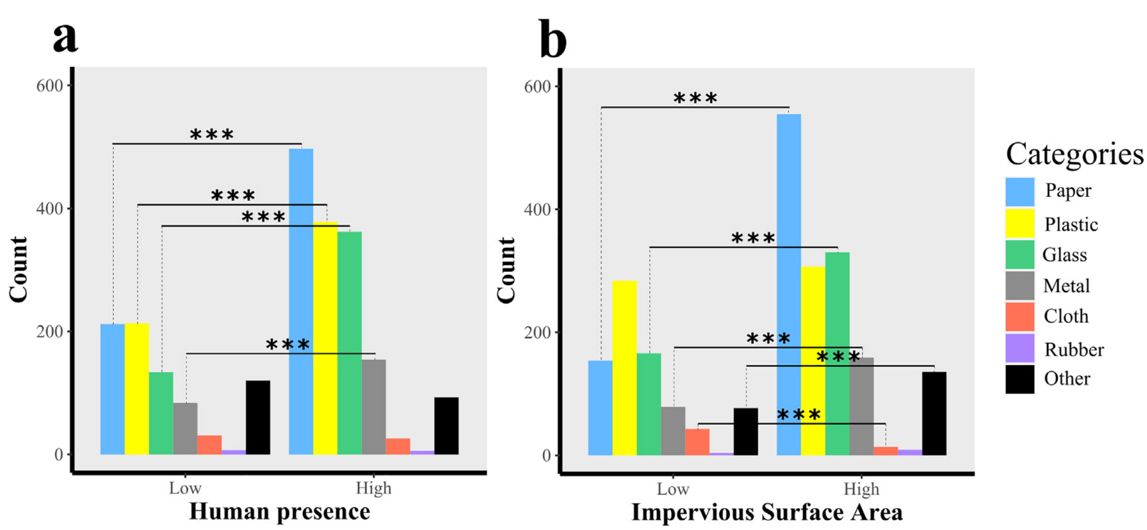

Fig. 2. Ground environmental solid waste pollution in contrasted levels of human presence and Impervious Surface Area (ISA) (Transect Data). Total number of solid waste items detected in the environment by surveying ground transects and grouped by contrasted levels of Human presence (a) and Impervious Surface Area (b), $N = 100$ nestboxes, corresponding to 300 ground transects. Low (mean ± se, 0.29 ± 0.03) and high (2.18 ± 0.23) levels of human presence included each 50 nestboxes. Low (mean ± se, 1.03 ± 0.2) and high (mean ± se, 24.7 ± 2.25) levels of ISA, included 50 nestboxes. Chi-squared tests of independence (χ^2) were run for each solid waste category ("Paper", "Plastic", "Glass", "Metal", "Cloth", "Rubber" or "Other") to compare contrasted levels (reported as "Low" versus "High") of human presence and urbanisation (ISA). Groups were characterised by the same number of sampling locations (i.e., $N = 50$ nestboxes per group). Only significant outputs are indicated ($p \leq 0.001$***).

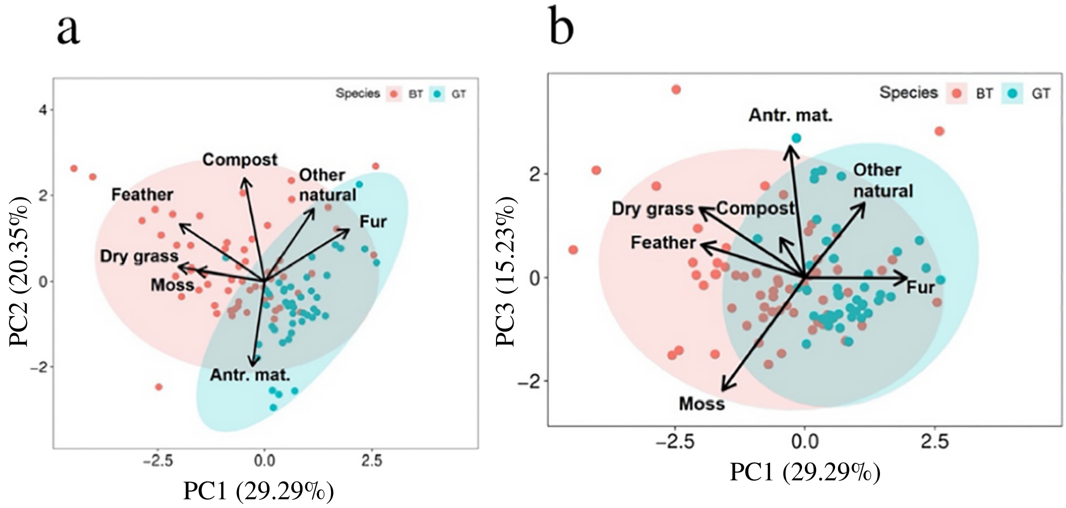

Fig. 3. Composition of great tit and blue tit nests (Nest Data, N = 100 nests, $N_{great\ tits}$ = 43; $N_{blue\ tits}$ = 57). PCA visualization of species-specific nest components in blue tits (red dots reflecting nests and ellipse reflecting empirical approximate 95% confidence region) and great tits (blue dots and ellipse) for PCA axes 1 and 2 (A) and PCA axes 1 and 3 (B).

environmental solid waste pollution (relative to nests from low levels of environmental solid waste pollution; $p < 0.005$; Fig. 4a, Table S8). Great tit nests also significantly differed in nest composition in contrasted levels of human presence (Fig. 4b, Table S8). Specifically, in great tit nests characterised by a higher human presence in their vicinity, we observed a significant, 1.46-fold increase in moss, a 0.6-fold decrease in animal origin material, and an impressive 6.8-fold increase in anthropogenic nest materials (Fig. 4b, Table S8). Interestingly, variation in urbanisation modelled in terms of impervious surfaces (low vs. high ISA) did not influence great tit nest design.

3.3.1.2. Blue tit. In blue tits, attributes of the urban space (solid waste pollution, human presence, ISA) did not strongly covary with nest design. However, we recorded a lower contribution of fur in nestboxes surrounded by lower levels of environmental pollution ($p = 0.005$; Fig. 4). We also recorded a higher contribution of fur in nests with higher ground environmental solid waste pollution, feathers in areas with higher human presence (though the proportion of animal origin components in the nest was not statistically different), and compost in more urbanised areas (ISA; Fig. 4, Table S8).

3.3.2. Anthropogenic materials in nest design

In both great tits and blue tits, we report a significant and negative relationship between the weight of anthropogenic materials and the weight of materials of animal origin. In other words, the more anthropogenic materials were found in the nest, the fewer the materials of animal origin such as fur and feathers (Table 1 and S9). In addition, the proportion of anthropogenic nest materials in great tit nests increased with higher values of human presence in the nestbox surroundings (Table S9 and S10). Interestingly, none of the other environmental parameters retained in the final models (such as rainfall, human presence, species-specific environmental solid waste in great tits, and ISA in blue tits) were associated with the weight of anthropogenic materials in the nest (Table 1, S9 and S10).

3.4. Age effects

While female age was retained in the final model inferring variation anthropogenic nest materials in great tits, the confidence intervals for this variable overlapped with zero (Table S11). Our results thus did not support any association between female age and the amount of anthropogenic nest materials in the nest, whether modelled as a proportion or as a weight (Tables S12 and S13).

3.5. Reproductive success and anthropogenic materials in nests

3.5.1. Great tit

In great tits, there was no relationship between the amount of anthropogenic materials in the nest and the number of hatchlings or fledglings (Table 2, S14-S16).

3.5.2. Blue tit

We detected a significant, negative relationship between the proportion of anthropogenic nest materials and blue tit number of hatchlings and fledglings (Tables 2, S14-S16, Fig. 5). Thus, a 10% increase in the proportion of anthropogenic materials in the nest was associated with a decrease in brood size of 2.2 hatchlings (5.04–7.57, 95% CI), which is equivalent to a *c.* 30% decline in reproductive success (Fig. 5a). Similar estimates were found at the fledging stage, where a 10% increase in the proportion of anthropogenic materials in the nest was associated with a decrease in fledging success by 2.0 fledglings (3.88–6.93, 95% CI), which is equivalent to a 27% decline in reproductive success (Fig. 5b).

4. Discussion

Our study demonstrates that the strength of environmental solid waste pollution in the city is unequivocally and positively associated with human presence and urbanisation intensity measured as a percentage of impervious surface area (Fig. 2). We also found a positive relationship between human presence and the amount of anthropogenic materials in great tit nests (Fig. 4 and Table S8). Crucially, avian nest design was altered in both urban great tits and blue tits, as we demonstrated a negative relationship between the amount of anthropogenic materials in the nest and those of animal origin, such as fur and feathers (Table 1). Equally importantly, anthropogenic materials (e.g. solid waste pollution) in the nest were found to have a strong, and negative relationship with reproductive success in blue tits, but not great tits (Table 2).

4.1. Factors associated with environmental solid waste pollution

Environmental solid waste pollution was higher in locations with higher human activity and with higher urbanisation (measured by ISA; Fig. 2). Our findings are one of the first empirical studies on solid waste pollution in the urban space, here reported at a fine spatial scale (but see Schuyler et al., 2021). Importantly, our data confirm the findings of Schuyler et al. (2021), who reported that the number of visible humans when measuring

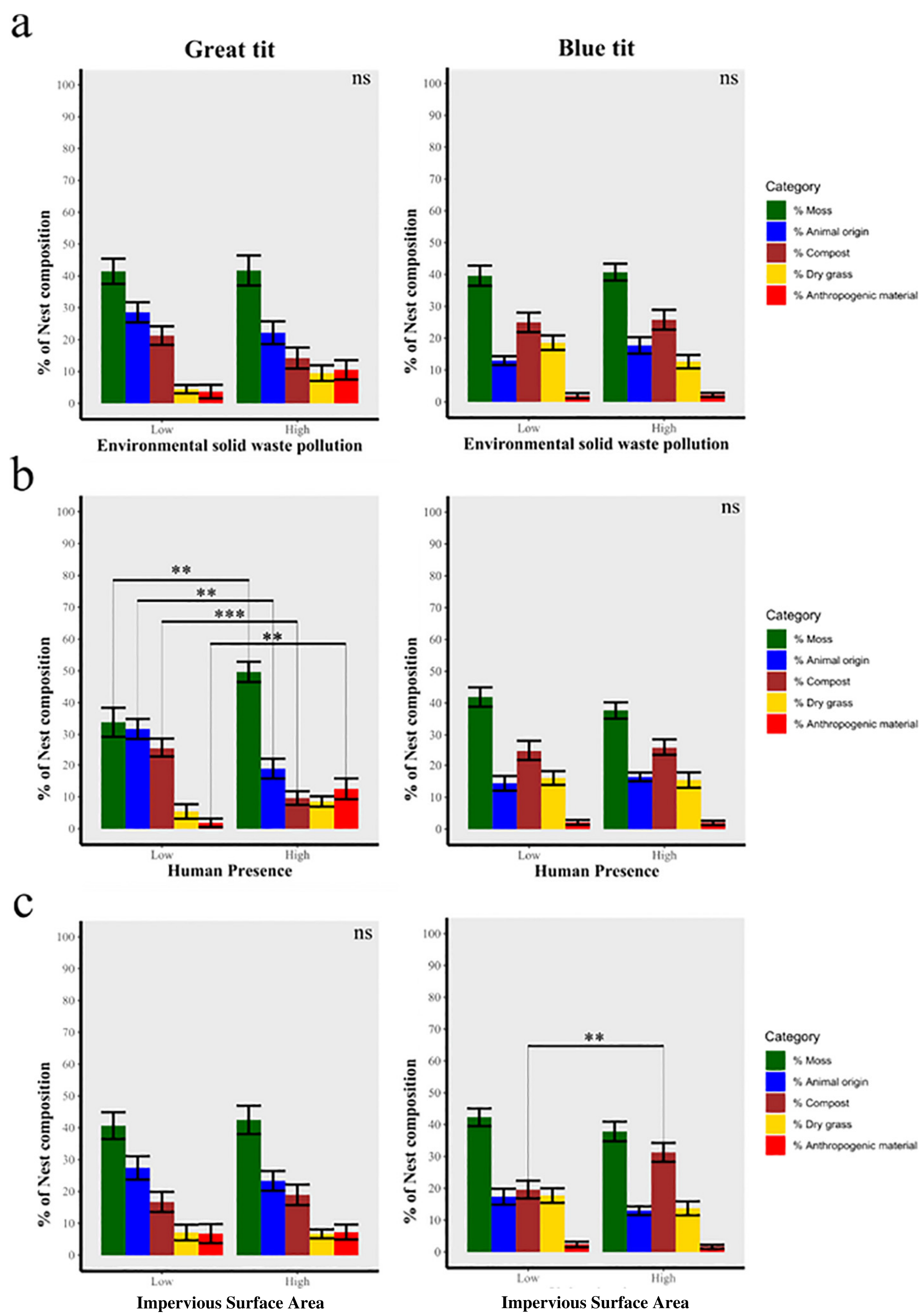

Fig. 4. Species-specific nest composition in the context of contrasted (a) environmental solid waste pollution, (b) human presence and (c) Impervious Surface Area (ISA) (Nest Data, N = 100 nests, $N_{great\ tits} = 43$; $N_{blue\ tits} = 57$). Barplots reporting the proportion of nest components relative to total nest weight in great tits and blue tits in contrasted levels of (a) ground environmental solid waste pollution, (b) human presence, (c) impervious surface area (e.g. urbanisation intensity). Welch-two-sample *t*-test results for great tits and blue tits are reported in Table S8. Significant *p*-values are indicated in bold ($p \leq 0.005$*, $p \leq 0.01$**, $p \leq 0.001$***). Note that the category "% animal origin" includes the categories "Fur" and "Feathers" combined.

solid waste pollution in the environment was positively associated with the number of solid waste items detected. Our findings also imply that measuring human presence with appropriate protocols designed to maximise repeatability whilst reducing time spent on the ground (Corsini et al., 2019) is an insightful tool to infer the distribution of solid waste pollution inland, especially when comparing fragments of the urban mosaic which are distinct in anthropogenic use.

We also report on a significant, positive relationship between urbanisation and environmental solid waste pollution in our system (Fig. 2). Our work provides an additional information layer on environmental solid waste pollution variation in the urban space. Specifically, thanks to the evaluation of 300 ground transects of urban environmental pollution, this study is a valuable reference for small-scale variation in environmental solid waste pollution that is usually difficult to obtain when only working with socioeconomic datasets. Poor prediction properties of socioeconomic datasets may be caused by the fact that, to date, most studies of environmental solid waste pollution use indirect evidence based on highly aggregated global socioeconomic datasets - such as population density, or Gross Domestic Products (GDP) (Barnes et al., 2009; Eriksen et al., 2014; Lebreton et al., 2017). By definition, aggregated datasets are of considerably lower spatial resolution, thereby preventing the same level of precision as reported here when exploring environmental solid waste variation in a

Table 1
Negative relationship between the weight of anthropogenic nest materials and those of animal origin in great tits and blue tits (in grams; Nest Data). In both species, the weight of anthropogenic materials in the nest increases with decreasing weights of animal origin components. Model: averaged summary statistics of Linear Mixed Effects Models (LMMs) testing the effect of ISA, human presence and environmental solid waste on the mass of anthropogenic materials (fitted as a Gaussian distribution) in great tits and blue tit nests. All global models included the following predictors: Impervious Surface Area (ISA, % of built-up areas in a 100 m radius), human presence, species-specific environmental solid waste identified on transects (transect solid waste), animal origin components (fur and feather mass in grams), rainfall and temperature. Study sites were fitted as random effect. Parameters with confidence intervals not overlapping 0 are reported in bold.

Species	Response	Variable	Estimate	se	CI 95%	Relative importance
Great tit	Weight of anthropogenic nest materials	Intercept	−1.366	0.713	−2.763; 0.031	
	N of nests = 32	**Animal origin**	**−1.032**	**0.404**	**−1.824; −0.239**	**1**
	Family = Gaussian	Rainfall	0.498	0.321	−0.131; 1.127	0.27
		Human presence	0.454	0.393	−0.317; 1.225	0.17
		Transect solid waste	0.454	0.478	−0.482; 1.39	0.17
Blue tit	Weight of anthropogenic nest materials	Intercept	−1.616	0.249	−2.104; −1.127	
	N of nests = 42	**Animal origin**	**−0.559**	**0.231**	**−1.012; −0.107**	**1**
	Family = Gaussian	ISA	−0.367	0.243	−0.842; 0.108	0.3

biological context. Our work also confirms previous work ran on a global dataset (Hardesty et al., 2021), where the authors demonstrate the crucial role of infrastructural networks, national wealth, and artificial light at night on increased levels of solid waste pollution inland. The same work highlights that solid waste pollution is heterogenous at a sub-national, local scale.

Data collection for this study took place in 2020, at the very start of the COVID-19 pandemic crisis. In Poland, the strictest lockdown measures prohibiting citizens from attending urban green areas occurred in April, and lasted for a 20 day-period (Dziennik Ustaw Rzeczypospolitej, 2019, Legislation nr 566 and nr 697). This timeframe largely overlapped with our data collection on environmental solid waste pollution, which started at the end of March and finished by the first week of May 2020 (at the same time, note that our measures of human presence, sampled multiple time and in a repeatable manner, were made prior to 2020; see Corsini et al., 2019). Unsurprisingly, solid waste items were still detected in the environment despite the important lack of human activity in the field for this short period: this indicates that short-term restrictions on human activities do not neutralize the consequences of human activities accumulated in the environment (such as the presence of solid waste pollutants) in the long run. Importantly, as human presence emerged as a temporally stable and generally repeatable dimension of the urban mosaic (Corsini et al., 2019), our findings further highlight the pervasive role of humans on solid waste pollutants distribution across human-dominated landscapes.

This study confirms that the urban habitat offers a unique opportunity to study and understand our impact on nature through the disposal of solid waste. As we are currently facing a global pollution crisis, more research conducted on the distribution and accumulation of solid waste inland, specifically in understudied habitats such as urban areas, is timely and much needed (e.g. Hardesty et al., 2021).

4.2. Species-specific nest composition

Nest dissection revealed significant differences in nest composition between great tits and blue tits (Fig. 3); these are in agreement with previous findings on the topic, reporting a greater amount of feathers and anthropogenic material in blue tit than in great tit nests (Britt and Deeming, 2011; Hanmer et al., 2017). Importantly, this study reports an important change in urban nest design pertaining to blue tits and great tits: in both species, there was a negative relationship between the amount of (i) dry grass, moss, feathers and fur, and (ii) anthropogenic materials in the nest (Fig. 3). These findings are further discussed in the context of the availability hypothesis below.

4.3. Mechanisms underlying the use of anthropogenic nest materials in birds

4.3.1. Availability hypothesis

Interestingly, environmental solid waste pollution detected on ground transects in nestbox vicinity was not retained in final models of anthropogenic materials variation in the nest (Table 1). This suggests that tits selectively pick anthropogenic materials for nest building, as only some solid waste categories found in the environment were incorporated by tits into nests. In both tit species, the anthropogenic materials most commonly found in nests included: cloth insulation materials, cloth threads, and plastic strings. It is possible that tits selectively choose these materials for their function (e.g. insulation, structure; Reynolds et al., 2019). Indeed, past work suggests that birds do not pick nesting material randomly (Bailey et al., 2014; Briggs and Mainwaring, 2019). In an experiment where artificially dyed wool was provided as nest material to four different species of tits (blue tit, great tit, coal tit *Periparus ater*, and marsh tit *Poecile palustris*), some great tit individuals flew considerable larger distances (>200 m) than

Table 2
Relationship between anthropogenic nest materials and fitness (Nest Data). Blue tit reproductive success decreases with an increasing proportion of anthropogenic nest materials in the nest. Model: averaged summary statistics of Linear Mixed Effects Models (LMMs) testing the effect of species-specific environmental solid waste on avian fitness. All global models included the following predictors: Impervious Surface Area (ISA, % of built-up areas in a 100 m radius), human presence (Human Presence), proportion of anthropogenic materials in the nest, species-specific environmental solid waste, animal origin components (proportion of fur and feathers), rainfall and temperature. Study sites were fitted as random effect. Parameters with confidence intervals not overlapping 0 are reported in bold.

Species	Response	Variable	Estimate	se	CI 95%	Relative importance
Great tit	N of fledglings per brood	Intercept	4.11	0.71	2.718; 5.502	
	N of nests = 39	Anthropogenic nest materials	0.786	0.577	−0.346; 1.918	0.44
	Family = Gaussian	Human Presence	−0.587	0.574	−1.711; 0.538	0.26
		Animal origin	0.343	0.601	−0.834;1.52	0.21
		ISA	0.005	0.543	−1.059;1.07	0.09
Blue tit	N of fledglings per brood	Intercept	5.354	0.764	3.857; 6.851	
	N of nests = 57	**Anthropogenic nest materials**	**−0.950**	**0.47**	**−1.872; −0.029**	**0.90**
	Family = Gaussian	Human Presence	−0.845	0.516	−1.857; 0.167	0.66
		Temperature	**0.564**	**0.529**	**0.176; 2.247**	**1**
		Rainfall	0.684	0.606	−0.505;1.872	0.35
		ISA	−0.166	0.541	−1.225; 0.894	0.1

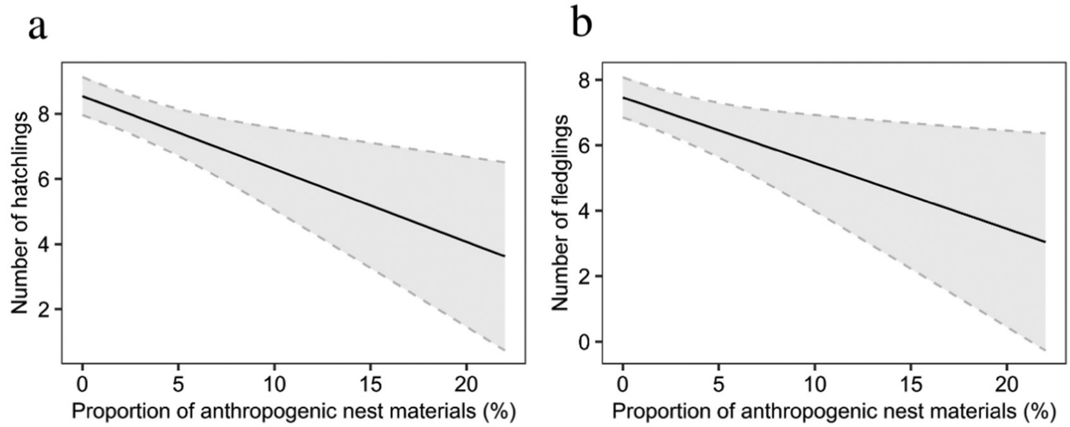

Fig. 5. Blue tit reproductive success decreases with increasing proportion of anthropogenic material in the nest (Nest Data). The prediction of increasing proportion of anthropogenic nest materials in nest on number of hatchlings (a) and fledglings (b) of blue tit.

other members of the population to select this specific material (Surgey et al., 2012). Further work is needed to confirm whether the proactive selection of anthropogenic materials generates an adaptive outcome, or whether it acts as an ecological trap at the reproductive level (Reynolds et al., 2019). Importantly, our study clearly shows a negative relationship between the amount of anthropogenic nest materials and reproductive success in blue tits (see Section 4.3.3 for more details).

A clear signal related to urban nest design that emerged for both species here investigated was the significant, negative association between the amount of anthropogenic nest materials and that of animal origin (fur and feathers). Although we did not measure the availability of fur and feathers in the environment, it is possible that their availability is reduced in places where there are high levels of human presence and are consequently replaced with anthropogenic nest materials. In nests collected from the forest, fur in nests mostly originated from wild animals, such as wildboars and deers (Z.J., pers. obs.), which are not that abundant in Warsaw city. It is worth noting that fur and feathers are the most insulating materials used in natural nest construction (Deeming et al., 2020), which leads to the possible assumption that, in urban tits, anthropogenic nest materials play a crucial insulating function. Yet, this requires further investigation, and we encourage further work to refute or confirm these trends, which would also strongly benefit from an experimental approach.

There are also some possible limitations of our results, as we quantified solid waste pollution only on the ground, whilst tits may also collect nesting elements in other places – from buildings, trash bins or backyard clothing lines. Such sources are all undeniably difficult to quantify. Also, we were only able to detect items visible to the human eye from a standing position, in order to comply with the CSIRO protocol guidelines for the Global Leakage Baseline Project. Detection efficiency is also likely to vary depending on the substrate, as it was easier to identify items on sand, asphalt, or bare ground and less so in thick vegetation such as tall grass or nettles.

4.3.2. Age hypothesis

Despite the fact that earlier studies showed a positive association between age and the presence of anthropogenic nest materials in long-lived avian species (Jagiello et al., 2018; Sergio et al., 2011), the *age* hypothesis was not supported by our findings. There are at least two reasons that may explain these results. First, great tits and blue tits are short-lived species in the wild, with a mean life expectancy of *c.* 2 years (Payevsky, 2006); thus, it is more likely that the age hypothesis gains greater functional meaning in long-lived species (Jagiello et al., 2018; Sergio et al., 2011) than in shorter-living ones. Indeed, experience plays a crucial role while collecting solid waste during the nest-building phase (Sergio et al., 2011). Second, such lack of association between nest composition and age may also be the result of the limited age partitioning possible for great tit and blue tit females. Indeed, age could only be established based on feather moulting characteristics, which only allows to establish two age groups (first-year breeder or older females); this contrasts with the use of a more diverse and continuous age variable used in earlier studies (Jagiello et al., 2018; Sergio et al., 2011).

4.3.3. Adaptive hypothesis – effect of anthropogenic nest materials on reproductive success

Our study revealed a significant, negative relationship between the amount of anthropogenic nest materials and blue tit reproductive success, but the causal relationship behind it requires further investigation. Crucially, this is the first study reporting reduced reproductive success (measured both in terms of number of hatchlings and number of fledged birds) in nests polluted with anthropogenic materials (Fig. 5, Table 2 and S15). These results also improve our understanding of the use of novel nesting materials of human origin (Reynolds et al., 2019).

Interestingly, nests with a higher contribution of anthropogenic materials were also poorer in terms of feathers and fur (Table 1). Our results suggest that feathers may be replaced by anthropogenic materials, which ultimately results in a negative reproductive outcome in the blue tit, as confirmed at two consecutive offspring developmental stages. From a functional perspective, feathers enhance thermal insulation (Windsor et al., 2013), protect against microbial infections (Ruiz-Castellano et al., 2016, 2019), and act as ectoparasite repellent (Deeming and Reynolds, 2016). Interestingly, Järvinen and Brommer (2020) reported that blue tit nestlings raised in feather-rich nests had a higher chance of recruitment to the breeding population. The authors suggest that in blue tits, it is more likely that feathers in the nest are used as an extended phenotype and signal of female quality. Thus, the process we report here – where blue tit nestlings are less likely to survive in nests rich with anthropogenic material (and feather poor; Fig. 5) is in agreement with reduced blue tit reproductive success as reported by Järvinen and Brommer (2020). At the same time, this pattern also highlights the anthropogenic interference driven by cities that is acting on the extended phenotype of birds.

Consequently, valuable further work is required to explore the relationship between parental quality, expressed phenotypically in terms of presence of anthropogenic materials in the nest, and fitness. Specifically, this study also highlights the need for an experimental framework to improve our understanding of these associations. More generally, these findings confirm considerable scope for exciting work on the impact of solid waste pollution on extended phenotypes and sexual selection in the urban space.

Anthropogenic materials used by great tits and blue tits in their nest mainly largely consisted of pieces of cloth, straps or plastic strings (Table S2), and are the irrefutable evidence of living in the Anthropocene. In all the nests here examined ($n = 100$), we did not record any nestling unequivocally harmed by anthropogenic nest materials, but for one case where a nestling had its wing entangled in human hair, and was gently detangled (Z.J., pers. obs.). In contrast to earlier reports (Suárez-

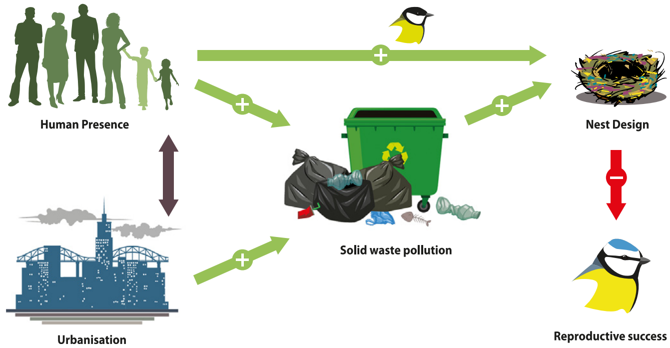

Fig. 6. Summary. An increasing number of humans are moving into cities, driving urban areas to expand in size. We demonstrate that human presence and urbanisation (modelled as impervious surfaces), assessed at a fine spatial scale, significantly covary with solid waste pollution in the environment. Moreover, we demonstrate a positive relationship between human-driven environmental solid waste pollution and the contribution of anthropogenic nest materials in great tit nest design. Importantly, we also report on a clear, negative relationship between anthropogenic nest materials (nest design) and blue tit reproductive success. Green and red arrows report on significant positive and negative relationships demonstrated in this study, respectively. The black arrow reflects the positive relationship between human presence and urbanisation as reported in Szulkin et al., 2020.

Rodríguez and Macías Garcia, 2014), the inclusion of cigarette butts was limited to only 10 nests (that is 10% of all investigated nests), and their amount, relative to other anthropogenic nest materials, was marginal. Therefore, we do not expect any considerable toxic effects from the *c.* 400 harmful substances present in cigarette butts (Suárez-Rodríguez and Macías Garcia, 2014) to have interacted with and / or enhanced the reported reduction in reproductive success in our blue tit population (Fig. 5). Future studies are needed to gain a finer understanding of the possible functions of anthropogenic nest materials in nest construction, and nest microclimate. Moreover, establishing causal links between anthropogenic nest materials, parental quality and avian fitness in the urban space will further allow assessing the possible role of these materials in generating ecological and/or evolutionary traps in the long run.

5. Conclusions

In this study, we showed a pervasive, negative relationship between environmental solid waste pollution and reproductive success. Specifically, environmental solid waste pollution driven by human presence emerged as key factor associated with anthropogenic materials in avian nests. Thus, in territories characterised by higher levels of human presence (undeniably the proximate cause for increased environmental solid waste pollution), great tits and blue tits included more anthropogenic materials in their nests, and fewer materials of animal origin (e.g. fur and feathers). Finally, anthropogenic nest materials were negatively associated with reproductive success in blue tits, but not in great tits, which highlights species-specific sensitivity to environmental pollution (Fig. 6). Further work targeting the functional role and fitness consequences of anthropogenic materials in avian nest design across a broader range of taxa and environments is crucial to determine the role of macroplastics on urban wildlife biology and to better inform waste policy management in the light of the acute global plastic pollution crisis we are currently facing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank the Wild Urban Evolution and Ecology Lab and all fieldworkers who participated in data collection during the challenging, pandemic field season of 2020. We are grateful to Andrzej Gajewski for developing the idea of the project in its early stage. We would like to thank two anonymous reviewers whose comments and suggestions considerably improved our initial manuscript. This study was funded by the Polish National Agency for Academic Exchange (NAWA), project numbers PPN/IWA/2019/1/00070 awarded to ZJ and PPN/IWA/2019/1/00069 awarded to MC, and by the Polish National Science Centre (NCN) with a Sonata BIS 2014/14/E/NZ8/00386 and OPUS grant 2016/21/B/NZ8/03082 awarded to MS, and by the Foundation for Polish Science (FNP) scholarship "START" awarded to ŁD. This research was carried out with a permit from the Regional Directorate for Environmental Protection (RDOS).

CRediT authorship contribution statement

ZJ: Conceptualization, Methodology, Data collection: life history, environmental pollution survey, nest dissection, Writing - original draft, Writing - review & editing. **MC**: Methodology, Data collection: life history, environmental pollution survey, Formal Analysis, Writing - review & editing. **ŁD**: Methodology, Formal Analysis, Writing - review & editing. **JDIA**: Writing - review & editing **MS**: Data collection: life history, Writing - review & editing. All authors edited and approved the final version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.156034.

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