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Nest composition of Blue Tits (*Cyanistes caeruleus*) along an urban gradient

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Abstract

Nests are structures that protect eggs and nestlings from the external environment while also serving various other functions in avian life histories. Nest-building behaviour varies between species and habitats, and recent work has highlighted that in areas with high human activity and low availability of natural nest material, birds may use anthropogenic material to construct nests. However, we know relatively little about how nest composition is affected by human presence along urban gradients. Here we examined how nest composition differed between urban and forest populations of Blue Tits *Cyanistes caeruleus*, and the impact that variation in nest composition had on reproductive success (clutch size, hatching and fledging success). We found a statistically significant decrease in the weight of moss and grass and an increase in anthropogenic materials in urban compared to forest nests. Nests initiated earlier in the urban environment showed a higher weight of anthropogenic materials. The weight of moss and grass was positively related to fledging success. Our results suggest that the use of anthropogenic material by urban birds might be a maladaptation, and/or that urban birds are constrained in the amount of moss and grass they can find during nest building. Future studies should aim to quantify the availability of material within the environment to test these non-mutually exclusive hypotheses.

Keywords: Blue Tit, anthropogenic nest materials, nesting behaviour, avian breeding

INTRODUCTION

The process of urbanization can have various impacts on ecosystems, such as the construction of artificial and impermeable structures, the elimination of natural vegetation (Ruas et al., 2022; Yan et al., 2019), the introduction of pollutants, including light and chemicals (Dominoni et al., 2013), and increased levels of human disturbance (Sol et al., 2013). This is followed by changes in ecological factors such as predation pressure (Eötvös et al., 2018), food availability (Marzluff, 2001) and temperature (due to the urban heat island effect) (Puppim de Oliveira et al., 2014). Whether a species can thrive in an urban environment depends on how it is affected by the changes brought about by its new habitat. Some animals can take advantage of the opportunities presented by urban environments and can survive or even thrive in cities. Some animals may not be able to tolerate the urban environment and may experience a population decline or avoid urban habitats (Kark et al., 2007; González-Lagos & Quesada, 2017; Corsini et al., 2021). Other animals can take advantage of the opportunities presented by urban environments and can survive or even thrive in them. However, to adjust to life in the city, changes in behaviour, physiology or genetic sequence may be required (Johnson & Munshi-South, 2017; Marzluff, 2001).

As nest building is a major part of an animal's life history, studies have suggested that nest composition may be affected by urbanisation (Reynolds et al., 2019). These changes can involve using less natural materials, altering the structure of the nest, and/or incorporating man-made materials (Antczak et al., 2010; Jagiello et al., 2019; Votier et al., 2011). Anthropogenic nest material refers to items not naturally found in nature but created by human actions. Materials such as plastic, string, and coir are examples of human-derived (anthropogenic) nest materials (Briggs et al., 2023). Incorporating anthropogenic nest materials has a positive correlation with the human footprint index (Jagiello et al., 2019). In urban environments, the availability of natural nest materials is often reduced, leading birds to use anthropogenic nest materials as a replacement (Wang et al., 2009). Birds residing in urban environments may incorporate more anthropogenic nest materials into their nests than birds residing in non-urban environments (Jagiello et al., 2019). This raises the question of why birds use anthropogenic materials and how it affects their life histories.

Jagiello et al. (2022) suggested three major hypotheses that explain anthropogenic material use in bird nests. Firstly, the availability hypothesis states that when the availability of anthropogenic materials is higher than natural materials, there will be increased use of the former. However, there is mixed evidence for this hypothesis. For example, a study that looked at the preference for nest material in Pied Flycatchers, *Ficedula hypoleuca,* found that when given a choice, the birds preferred natural material over anthropogenic nest materials (Briggs et al., 2023). Secondly, the age hypothesis proposes that the age of parent birds and their experience are connected to the use of anthropogenic material, where older and experienced birds use it as an extended sexual signal (Jagiello et al., 2022; Sergio et al., 2011). A study in Black Kites, *Milvus migrans,* showed that older birds incorporated more plastic material in their nests up to the age of 10-12 years, their prime reproductive age, and they reduced or even stopped using plastic after this age. This suggests that the use of plastic in this species might be used as a signal of sexual quality (Sergio et al., 2011). Finally, the functional hypothesis states that the functional advantage of anthropogenic materials leads to their use in nests (Sergio et al., 2011; Suárez-Rodríguez et al., 2013). Several advantages have been reported with the use of human-derived materials in bird nests. Plastic strings can play a role in enhancing the nest structure, which is a key factor in safeguarding the eggs and fledglings from harsh weather elements like the wind (Reviewed by Deeming, 2023). Manipulating human-derived materials, such as synthetic threads, during nest building could be easier and could lead to lower energy expenditure than manipulating natural alternatives (Esquivel et al., 2020). Cigarette butts are found to have a repelling effect on ectoparasites compared to natural nest materials, which could decrease the number of ectoparasites found in city bird nests if cigarette butts are included in nest construction (Suárez-Rodríguez et al., 2013).

There are also several potential negative impacts of anthropogenic nest materials. Modifications of nests might alter their structural and functional properties, including integrity, camouflage and thermoregulation (Mainwaring et al., 2014; Lopes et al., 2020). Suárez-Rodríguez et al. (2013) investigated the effects of the presence of cigarette butts in nests and the effects on breeding success. They found that even though cigarette butts have ectoparasite-repellent effects, the number of cigarette butts in the nest was positively associated with the level of female genotoxic damage in House Finches, *Haemorhous mexicanus,* during breeding. The study also found that the negative effects of cigarette butts on the breeding success of urban birds outweigh any potential benefits from ectoparasite repulsion (Hanmer et al., 2017; Suárez-Rodríguez et al., 2013). Plastic waste can also cause chemical harm through the release of toxins, leachates, and non-degraded persistent organic pollutants, which can enter food webs via a process known as trophic transfer (Teuten et al., 2009). The inclusion of plastic in nests can lead to the entanglement of chicks, as reported in a study on Northern Gannets, *Morus bassanus* (Votier et al., 2011). In American Crows, *Corvus brachyrhynchos,* breeding success was lower in nests with higher amounts of plastic. A major reason for the reduction in breeding success was the entanglement of the chicks and they identified this as a major threat (Townsend & Barker, 2014). A similar case of strangling was reported in Great Grey

Shrikes, *Lanius excubitor*, and it is suggested that both adults and the chicks are prone to strangling (Antczak et al., 2010). Camouflage is an important nest characteristic to prevent nest predation, which is a major cause of nest failure (Corrales-Moya et al., 2023). Antczak et al. (2010) noted that, in Great Gray Shrikes, nests containing plastic string were more easily detected by predators. In a study on Clay-coloured Thrush, *Turdus grayi*, the proportion of the outer layer of the nest covered by anthropogenic nest materials was negatively correlated with the nest's daily survival rate, indicating that the more exposed anthropogenic nest materials, the higher the chance of it being predated (Corrales-Moya et al., 2023). The findings revealed that variations in the nest dimensions did not affect predation events, while the only factor that had an effect was exposed anthropogenic nest materials. Plastic is considered a thermal insulator; higher incubation temperatures and increased heart rates were observed in nests with higher plastic content (Veríssimo et al., 2024). Such effects may cause heat stress, especially in hotter regions.

Although several studies have looked into the effect of anthropogenic materials on breeding success, most of these have focused on marine habitats and seabirds, and only a few have focused on passerines (Jagiello et al., 2019). A study on Blue Tits, *Cyanistes caeruleus,* and Great Tits, *Parus major,* found that the presence of anthropogenic materials was negatively correlated to breeding success in Blue Tits but not in Great Tits (Jagiello et al., 2022). Increase in the use of anthropogenic materials has been seen over a two-year comparison study that included Great Tits and Blue Tits (Girão et al., 2024). Green nest materials, such as aromatic plants in nests, help reduce ectoparasites and help strengthen nestlings' immune systems (Gwinner & Berger, 2005; Tomás et al., 2012). Feathers in nests are associated with increased thermal regulation and resistance against microbial and ectoparasite infections (Järvinen & Brommer, 2020). Hence, the use of anthropogenic materials instead of feathers might have implications for reproduction and fitness. On these accounts, Jagiello et al. (2022) suggested that the chicks from feather-rich nests have a higher chance of recruitment to the breeding population. Animal hair and wool also serve a similar purpose to feathers in providing insulation, which reduces energetic cost for parents (Harničárová & and Adamík, 2016; Surgey et al., 2012).

In the current study, we aim to investigate 1) the effect of urbanization on nest composition and 2) the relationship between habitat, nest composition and breeding success. To this end we collected nests and breeding data from Blue Tits breeding at nine sites between the city centre of Glasgow and a forest approximately 35 miles away in the Loch Lomond and Trossachs National Park, UK. We predicted a higher quantity of anthropogenic materials in the urban nests. Specifically, we predicted that nests with higher amounts of anthropogenic material would produce fewer nestlings than nests with higher natural material content.

MATERIALS AND METHODS

Study species and monitoring of breeding success

The Blue Tit is a small passerine widely distributed in Europe and Western Asia. They are cavity nesters and are usually found in deciduous to mixed woodlands and urban parks, and gardens. They usually have a life span of three years and start reproducing at the age of one year (Stenning, 2018). In Scotland, Blue Tits begin building nests in late-march to early-april, and the breeding season lasts until late-June. Nest building is primarily carried out by females, which uses multiple materials such as moss, feathers, and animal hair (Britt & Deeming, 2011). Clutch size ranges between 4 to 14 eggs, where one egg is laid per day (Perrins, 1990). In Scotland, Blue Tits only lay one clutch. The incubation time ranges between 10 days and three weeks (Gibb., 1950). Once the chicks are hatched, provisioning is shared by both parents, and fledging happens around 15-20 days post-hatching (Fargallo & Johnston, 1997).

The study was carried out along an urban-rural gradient in Scotland, using nine sites spanning a 56km transect from the city centre of Glasgow (55.8668° N, 4.2500° W) to the woods around The Scottish Centre for Ecology and the Natural Environment (SCENE) on the east banks of Loch Lomond (56°7’44”N 4°36’46”W). Over the past few decades, approximately 500 Schwegler Woodcrete nest boxes with a 32mm entrance diameter have been placed along this gradient and monitored. For the current study, nest boxes were monitored across all sites from April 1st to June 15th, 2023. Starting from April 1st, all the boxes were checked once a week to assess the progress of the nest building and incubation. The first egg date was recorded as the day of the year when the first egg was laid. When nests were expected to hatch, we started to check the active nest every other day until chicks were found. Once the chicks had fledged, the data for breeding success was collected by counting the number of unhatched eggs and dead chicks. The nests (n=64; rural=33, urban=31) were collected in plastic zip-lock bags for dissection and analysis.

Nest collection and dissection

A total of 64 nests were analysed (rural = 33, urban = 31). Once the nests were collected, they were frozen for at least 12 hours to reduce the activity of arthropods, and they were kept frozen until the time of dissection. Before dissection, the nests were dried in a heat chamber at a temperature of 50 degrees Celsius for at least 12 hours to prevent moisture in the nests. Once dried, the nests were dissected, and the material assigned to a category and measured to an accuracy of 0.001 g. The nest materials were grouped

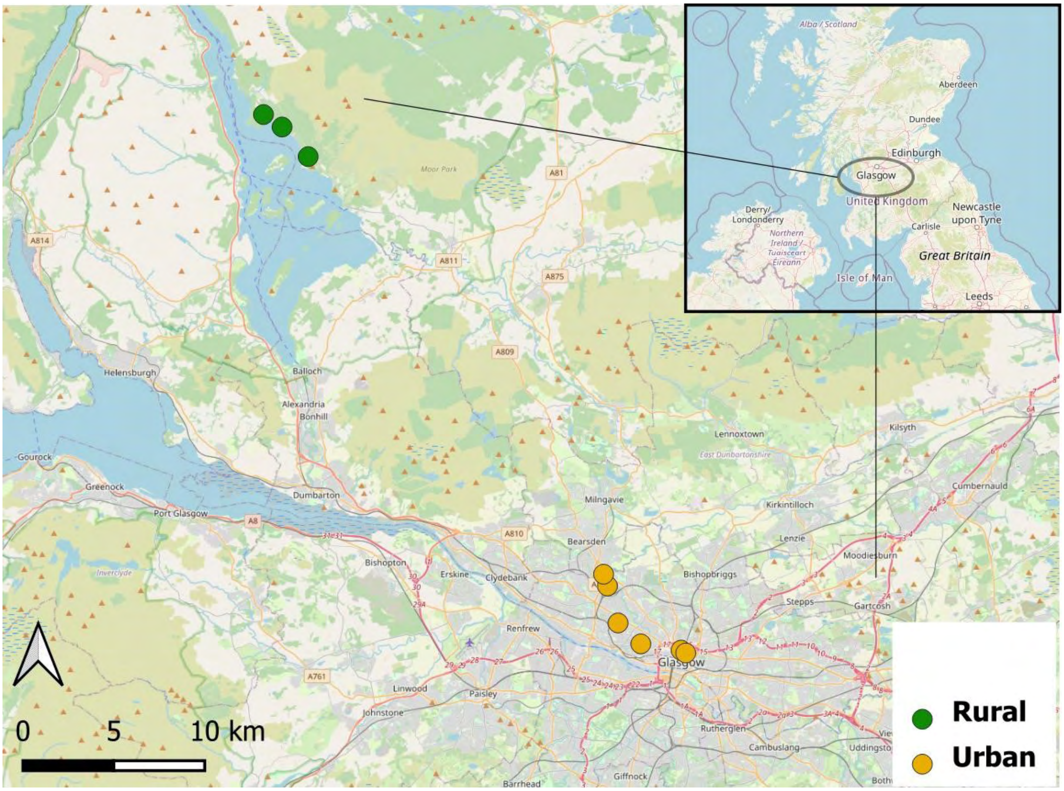

Figure 1. Map of study sites. The points represent different sites where nests were collected, with rural sites shown in green and urban sites in yellow. From six urban sites and three rural sites, a total of 64 nests (rural = 33, urban = 31) were collected. A detailed table and interactive map of the sites can be found in the supplementary materials.

into four categories: 1) moss and grass, 2) feathers, 3) wool and hair, and 4) anthropogenic material; together, they will be referred to as nest materials from now on (an image of each class can be found in Supplementary Fig. 1). The materials are intertwined intricately in the nests, and maximum effort was taken to separate them into each category.

Figure 2. Images of nests with anthropogenic materials. The nest on the left has a cup built largely from man-made fibers and the one on the right has fibers of multiple colors.

Environmental variables

Habitat was defined as a categorical variable with two levels (urban and rural) to represent the habitat in which the nests were collected. We also extracted the impervious surface area around a 100 m radius (IS100 from now on). The IS100 value represents the percentage of impervious surface area within a 100 m radius centred on each nestbox. This measure was calculated from Copernicus Land Monitoring Service, 2018, which captures the extent of non-permeable surfaces such as roads, buildings, and other urban infrastructure (*Copernicus Land Monitoring Service*, 2018; Jagiello et al., 2022).

Statistical analysis

The statistical analysis was performed using R version 4.3.3 (R Core Team, 2024). The analysis was conducted in two parts, corresponding to changes in nest materials and their effects on breeding success. In both parts, model selection was carried out via Akaike Information Criterion (AIC), and Interaction terms were removed if not statistically significant and if their removal improved model fit. The sJPlot package (version 2.8.16; Lüdecke, 2024) was utilised to visualize model predictions.

Nest Materials: To assess environmental effects on nest composition, we used Linear Mixed-Effects Models (LMMs) with each nest material type as the response variable and site as a random variable. Two sets of models were run for each nest material type, with the following fixed effects: 1) habitat (categorical: urban or rural), first egg date (continuous) and their interaction; 2) IS100, first egg date and their interaction. We did so because habitat was collinear with impervious surface area, but we still wanted to distinguish between the effect of habitat *per se* versus the effect of a specific environmental variable that might better function as a proxy of human activity and, thereby, the use of anthropogenic materials in nests.

Breeding Success: We considered the effect of urbanisation on clutch size, hatching success (calculated as the number of hatched eggs divided by clutch size) and fledging success (calculated as the number of fledglings divided by the number of hatched eggs). Clutch size was modelled with a Poisson GLMM, while hatching and fledging success were modelled as proportions of clutch size with binomial GLMMs with logit link functions. This was to account for the effect of clutch size on the success parameters. In all models, nest material type (weight of each material in grams) and first egg date were included as fixed effects, and site as a random effect.

RESULTS

Nest materials

Our analysis revealed no statistically significant effect of habitat (as a categorical variable, urban *versus* rural) or first egg-laying date on variation in the weight of nest material categories (Supplementary Tab. S3.1 to S3.6). The interaction between habitat and first egg date showed a marginally statistically significant variation in anthropogenic material per nest, indicative of a negative effect of first egg laying date on the weight of anthropogenic material per nest for the urban environment (estimate = -0.05, P = 0.03. Egg-laying dates did not appear to be correlated with variation in anthropogenic materials in rural nests (Fig. 4, Tab. 1).

We then assessed the effect of urbanisation as a continuous variable (i.e., the amount of impervious surface within a 100 m radius around each nest location) rather than as a dichotomous variable (habitat) on the mass of each nest material type. In all models, the interaction between the first egg-laying date and impervious surface area in 100 m was not statistically significant and hence, interaction terms were removed (Supplementary Tab. S4.1- S4.5). The first egg date was

Table 1- Output of linear mixed effect model used to assess the effect of habitat and first egg laying date on the weight of anthropogenic materials, with site added as a random effect.

Characteristic	**Estimate**[1]	**SE**[2]	**95% CI**[2]	**p-value**
Intercept	-0.06	4.88	-9.9, 9.7	>0.9
First Egg Date	0.00	0.041	-0.08, 0.08	>0.9
Habitat				
Rural	—	—	—	
Urban	12	6.13	-0.41, 24	0.058
First Egg Date* Habitat				
First Egg Date * Urban	-0.09	0.052	-0.20, 0.01	0.077

[1]*p<0.05; **p<0.01; ***p<0.001

[2]SE = Standard Error, CI = Confidence Interval

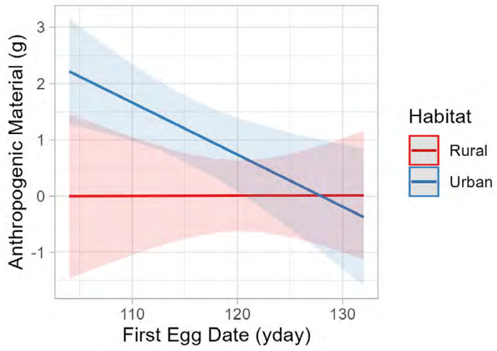

Figure 3. Predictions of a model explaining variation in anthropogenic nest material as a function of habitat and first egg date (y-day- count of days after January 1). The solid lines represent fitted linear regression, and the shaded area represents 95% confidence intervals.

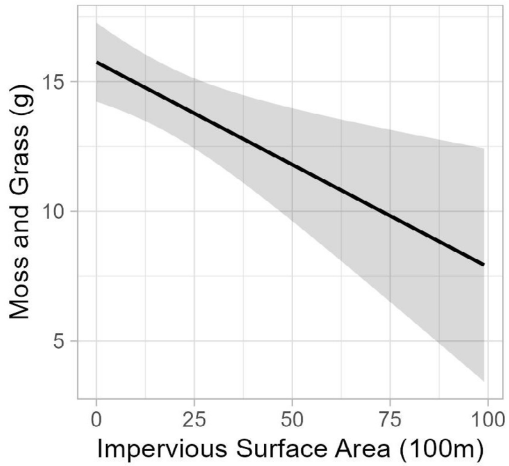

Figure 4. The predictive graph of the change in the weight of moss and grass with an increase in impervious surface area in a 100m radius, the solid line represents fitted linear regression, and the shaded area represents 95% confidence intervals. There is a statistically significant reduction in the weight of moss and grass with the increase in the amount of impervious surface area.

negatively correlated with the weight of anthropogenic materials (estimate = -0.42, $P < 0.01$; Tab. 2). In the case of moss and grass, IS100 showed a statistically significant negative trend with the increase in IS100 (estimate = -2.00, $P < 0.01$; Fig. 5, Tab. 3).

The total nest weight across habitats ranged from 7.5 g to 37.0 g, with a mean of 20.0 g (SD = 6.0). In rural habitats, the total weight had a mean of 18.0 g (SD = 5.0), while urban nests were heavier on average, with a mean of 22.0 g (SD = 7.0). Urban nests also showed greater variability in total weight, with heavier nests driving both the mean and median higher.

Anthropogenic material was present in 45.5% of rural nests and in 90.3% of urban nests, with an overall presence in 71.9% of nests across both habitats (Fig. 3). The weight of anthropogenic material ranged from 0 g to 7.9 g, with a mean of 0.5 g (SD = 1.3). It was nearly absent from rural nests, which had a mean of 0.0 g (SD = 0.1), whereas urban nests contained a mean of 0.9 g (SD = 1.7). The weight of moss and grass ranged from 4.8 g to 29.0 g, with an overall mean of 14.4 g (SD = 5.1). Rural nests had a higher mean moss and grass weight of 15.4 g (SD = 5.1), compared to 13.3 g (SD = 4.9) in urban nests. Feather weight was lower in rural nests,

Table 2- Output of linear mixed effect model used to assess the effect of impervious surface area within 100 m (IS100) and first egg laying date on the weight of anthropogenic materials, with site added as a random effect.

Characteristic	**Estimate**[1]	**SE**[2]	**95% CI**[2]	**p-value**
Intercept	0.59	0.245	-0.02, 1.2	0.056
First Egg Date	-0.42*	0.160	-0.74, -0.09	0.012
IS100	0.20	0.201	-0.23, 0.63	0.3

[1]*p<0.05; **p<0.01; ***p<0.001

[2]SE = Standard Error, CI = Confidence Interval

Table 3- Output of linear mixed effect model used to assess the effect of impervious surface area 100m and the first egg laying date on the weight of moss and grass, with site added as a random effect.

Characteristic	**Estimate**[1]	**SE**[2]	**95% CI**[2]	**p-value**
Intercept	14***	0.635	13, 16	<0.001
First Egg Date	-0.38	0.668	-1.7, 0.95	0.6
IS100	-2.0**	0.668	-3.4, -0.69	0.004

[1]*p<0.05; **p<0.01; ***p<0.001

[2]SE = Standard Error, CI = Confidence Interval

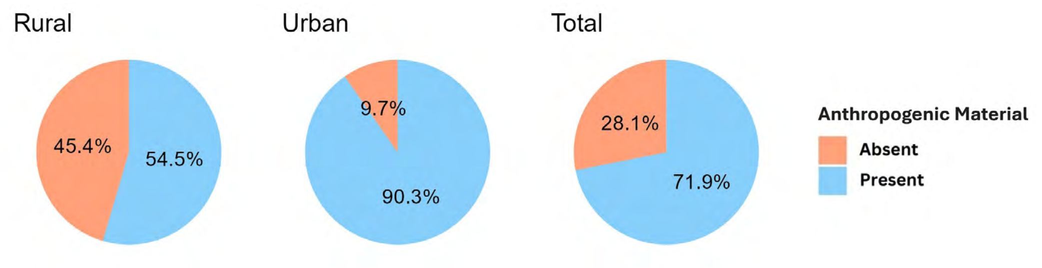

Figure 5. Pie charts illustrating the presence of anthropogenic materials in nests and the number of nests containing anthropogenic materials are presented. There was anthropogenic material in half of the rural nests, while 90.32% of urban nests had anthropogenic materials in them. In total, three-quarters of the nests had anthropogenic materials.

with a mean of 0.9 g (SD = 1.2), than in urban nests, which had a mean of 1.2 g (SD = 1.2). Lastly, wool and hair weights ranged from 0 g to 11.4 g, with a mean of 2.3 g (SD = 2.7). Rural nests had a mean of 1.3 g (SD = 1.8), while urban nests had more wool and hair, with a mean of 3.4 g (SD = 3.1) (Supplementary Tab S2).

Breeding success

The models with nest materials and first egg date showed no statistically significant results for clutch size and hatching success (Supplementary Tab. S5.1 and S5.2). However, for fledging success, the model selection indicated that the best model was the one with only moss and grass. In this model, the weight of moss and grass showed a positive effect on fledging success with a marginally statistically significant p-value (estimate = 0.27, P = 0.06), Fig. 6; Tab. 4).

Figure 6. Predictive graphs on fledging success and the variation in the weight of moss and grass. The solid line represents fitted logistic regression, and the shaded area represents 95% confidence intervals. Fledging success increases with an increase in the weight of moss and grass

Table 4. Output of generalised linear mixed effect model (logit link) assessing the effects of moss and grass weight and first egg date on fledging success (proportion of fledglings per clutch), with site included as a random effect.

Characteristic	**log(OR)**[1,2]	**SE**[2]	**95% CI**[2]	**p-value**
Intercept	-8.2	9.35	-26, 10	0.4
Moss and grass	0.27	0.147	-0.02, 0.55	0.069
First Egg Date	0.06	0.077	-0.09, 0.21	0.4

[1]*p<0.05; **p<0.01; ***p<0.001

[2]OR = Odds Ratio, SE = Standard Error, CI = Confidence Interval

DISCUSSION

This study provides evidence that urbanization influences nest material selection in blue tits and this might be marginally affecting fledging success. Also, egg-laying dates affect the amount of anthropogenic materials in the nests. We found that the urban nests had high variability in total nest weight and contained more anthropogenic materials. Considering the various nest materials, moss and grass were the only materials that showed a statistically significant reduction with an increase in impervious surface area. Total weight and wool, and hair also showed a reduction with the amount of impervious surface, but this result was not statistically significant. The weight of moss and grass was a marginal predictor of fledging success: nests that contained more moss and grass fledged more young. Conversely, anthropogenic materials were not associated with breeding parameters. This underlines the importance of natural materials especially “moss and grass” for reproductive fitness in Blue Tits.

Preferential selection of materials in urban and rural habitats?

The weight of anthropogenic materials in urban nests was higher than their weight in rural nests, while reproductive success and clutch size are known to be lower in urban compared to rural nests. Despite these trends, we did not find any statistical evidence for an association between anthropogenic materials and reproductive success. Also, it is to be noted that 72% of all the nests had anthropogenic material in them. We have noted that in urban nests, anthropogenic materials and wool/ hair materials were mostly used to provide structural support instead of grass, which was more common in the rural nests (J.

Roy pers. obs). The reduced availability of grass in the urban environment might be the reason for birds to use anthropogenic materials in their nests, or, following the availability hypothesis, anthropogenic materials may be more available in the urban environment than natural materials. The selective picking of nesting material was demonstrated by Briggs et al. (2023). While our study showed a reduction of moss and grass and an increased use of anthropogenic materials with increasing urbanization, it needs to be confirmed whether these patterns are a result of materials being actively selected by birds in urban areas or the result of lower availability of these materials. Thus, quantifying the availability of different types of materials will be crucial in future studies. This is particularly important when considering that the weight of anthropogenic materials was shown to increase the number of unhatched eggs in previous studies (Jagiello et al., 2022; Reynolds et al., 2019). In the review Reynolds et al. (2019) suggested city and site specific differences in nesting behaviours. Moreover, the changes we have observed may also be due to differences in the availability of materials within and between sites. Within sites, micro-habitat differences surrounding each nesting location might lead to differential selection of nest materials. Suárez-Rodríguez et al. (2013) reported cigarette butts used in Blue Tit nests as an insect repellent, but no nests in our sites had cigarette butts in them, which could be a city specific difference.

Anthropogenic materials as an extended sexual phenotype

Several theories have attempted to explain the reasons why birds incorporate anthropogenic materials in their nests, one of which is the sexual selection theory. When provided with natural materials, Black-Faced Spoonbills, *Platalea minor,* showed a preference for natural materials over anthropogenic nest materials (Lee et al., 2015). Surgey et al. (2012) suggest that the selection of wool-like artificial material is opportunistic. However, in our study, the three rural sites were oak woodlands with ample amounts of natural materials, and anthropogenic materials were scarce and mostly made up of trash from occasional tourists (J. Roy pers. obs.). Despite the lower availability of anthropogenic material, 54% of rural nests had anthropogenic materials in them. The presence of anthropogenic materials in the rural nests, despite natural materials being readily available, may suggest preferential selection towards anthropogenic material in rural habitats, as observed by Briggs et al. (2023). As previous studies have suggested, birds tend to use anthropogenic materials as an extended sexual phenotype (Jagiello et al., 2022). In the case of rural habitats, the anthropogenic materials were mostly used along with feathers as lining, which might play a decorative role in the nests, while in urban habitats, it was mostly added into the structural parts of the nests instead of grass (J. Roy pers. obs.). It can also be noted that the weight of anthropogenic materials was considerably lower in rural nests compared to urban nests. Thus, selective preference of anthropogenic materials in rural nests could point to this behaviour as an extended sexual phenotype, as suggested by Jagiello et al. (2022), while in urban nests might support the functional hypothesis.

Effects of parental phenotype on the selection of nest materials

Anthropogenic material was present in 90% of urban nests, whereas the weight of anthropogenic material in rural nests was nearly zero. The reason urban birds use anthropogenic material in their nests cannot be determined without quantifying the availability of natural nesting material in urban habitats. Although there was a marked increase in the amount of anthropogenic material in urban nests, breeding success was mostly driven by the weight of the moss and grass. Mainwaring & Hartley (2008) showed a reduction in cup lining with the progress of the breeding season, which shows a similar trend to the current observation in anthropogenic materials, which might be used as a cup lining. Earlier lay dates, larger and heavier nests, higher amounts of feathers, and the addition of aromatic plants are considered to correlate positively with parental traits such as age and experience (Mainwaring et al., 2008; Tomás et al., 2013; Williams et al., 2024). These act as sexual signals to elicit increased allocation by males, which is shown to improve breeding success (Tomás et al., 2013). In the urban habitat, nests built earlier in the breeding season had a statistically significantly higher weight of anthropogenic material, while in the rural habitat, the weight of anthropogenic materials remained low throughout. Since anthropogenic materials are higher in earlier urban nests, it is worth noting that early breeding parents might be selecting these materials as an extended sexual phenotype or using them as a substitute for natural materials due to availability or preference (Deeming, 2023; Jagiello et al., 2022).

Limitations and future directions

In this study, we cannot conclude whether urban and rural birds selected natural vs anthropogenic material actively, either for structural or sexual selection benefits, or due to differential availability of materials in urban and rural habitats. To distinguish between these different hypotheses, future studies could focus on quantifying the availability of each material in the micro-habitat surrounding and relate this to the proportion of each material included in the nest construction. Moreover, performing experiments to manipulate the presence and location of anthropogenic materials in the nest might shed light on whether their use may act as an extended sexual phenotype.

DATA AVALAIBILITY STATEMENT

The dataset supporting this study, Data for Nest Composition of Blue Tits (*Cyanistes caeruleus*) along an Urban Gradient, is

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Author contributions

Joseph Roy: conceptualization, methodology, formal analysis, original draft preparation, review & editing. **Claire J. Branston**: data curation, writing – review & editing; **Pablo Capilla-Lasheras**: data curation, writing - review & editing; **Paul J. Baker**: data curation. **Davide M Dominoni**: conceptualization, methodology, original draft preparation, writing - review & editing, supervision.

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