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Research article

Nest-boxes alter the reproductive ecology of urban cavity-nesters in a species-dependent way

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Human-provided nesting shelters such as nest-boxes mitigate the shortage of natural breeding sites. Since artificial nests are not where animals evolved and optimised their reproductive performance, it remains inconclusive if these are adequate substitutes, ensuring equivalent fitness returns while breeding. In particular, most knowledge on the ecology of cavity-nesting birds comes from nest-box populations, but no study has directly compared fitness consequences of breeding inside nest-boxes in relation to natural cavities in cities. We directly compare the reproductive performance, life-history trait variation and fitness consequences for two small passerines, blue and great tits, breeding in nest-boxes as opposed to natural cavities in an urban deciduous forest. We use a quasi-experimental setting to comprehend the conservation potential of these artificial cavities and to support/question generalisations stemming from nest-box studies. We show that the effects of cavity type vary between species: in blue tits, fitness proxies were negatively affected by nest-boxes (lower fledging success and fledgling numbers, longer time spent in the nest and later fledging date relative to natural cavities), while in great tits, the fitness proxies were unaffected by cavity type. Importantly, we detected accelerated incubation in both species breeding in nest-boxes. No differences in pre-hatching traits (lay date, clutch size, hatching rates) between cavity types suggest that the fitness deterioration occurred because of post-hatching effects. We highlight the ecological importance of old-growth tree stands, providing natural cavities for city-breeding animals and the need for quantifying alterations of reproductive ecology in other taxa using human-provided nests. Owing to the detected cavity type-dependent variation in reproductive performance, we support the criticism regarding the unconditional extrapolation of evolutionary and ecological interpretations of nest-box studies to general populations.

Keywords: city birds, life-history traits, natural cavities, nest-boxes, phenology

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Introduction

Anthropogenic landscape modifications occur at many levels and alter the use of habitat by wildlife (Cisneros et al. 2015, Magioli et al. 2019). Such alterations are of direct importance for planning conservation actions and for the study of ecological dynamics, but are also of concern for the general public interested in wildlife living on their doorstep. One notable example of habitat modification is the provision of artificial nesting places. The biological impact of such actions may be controversial since its relevance to phenotype and fitness variation occurring in natural breeding places remains understudied. Notably, many human-provided nests are used by hole-nesting birds that naturally breed in tree cavities. Natural cavities can be formed by wood decomposition and/ or breaking followed by microorganism colonisation, or as a result of active excavation by species of primary excavators (e.g. woodpeckers; Bovyn et al. 2019). Abandoned cavities can thus be reused by other cavity-nesters unable to excavate on their own (Wiebe et al. 2020). As such, natural cavities provide shelters for many passerine birds to rear their young and are superabundant in natural forests (Wesołowski 2007). However, in areas lacking old-growth tree stands in which natural decomposition takes place and with a lower number of active excavators, nest-boxes are offered as a conservation measure to increase breeding opportunities (Hacker and Gaines 1997, Tomasevic and Marzluff 2017). In some cases this is beneficial, increasing breeding probability (Sumasgutner et al. 2020), but in other instances increasing local densities may boost competition among birds using the same type of cavity (Newton 1994a, Diamond and Ross 2019). Moreover, the numbers of dominant species can affect the numbers and distribution of other birds, especially in secondary forests. In extreme situations, a species may become absent from areas where all suitable nests are taken by dominant competitors (Newton 1994a). The use of nest-boxes has much potential as a conservation tool, but only if we possess knowledge of the fitness consequences of breeding inside nest-boxes as opposed to alternative nesting cavities.

More generally, this leads to the need for a greater understanding of the use of nest-boxes for ecological studies in wild populations. Undoubtedly, nest-box-based studies benefit from the convenience of sampling. In contrast, studying birds in natural cavities requires considerable effort related not only with nest search, but also with accessing cavities situated in high places or with narrow entrances. For these reasons, nest-box studies are performed by a vast majority of researchers and have consequently become a standard from where the bulk of hole-nesting passerine biology data are collected. Yet, nest-boxes are not the breeding sites in which these birds originally evolved. Thus, nest-box populations may not be accurate models for general populations. Moreover, in the absence of natural nesting sites, such interventions are likely to promote species that may benefit from breeding in nest-boxes, while creating a possible ecological trap for other species that may suffer a decrease in reproductive performance in nest-boxes.

Only a handful of studies have directly compared fitness consequences of breeding inside nest-boxes in relation to natural cavities. Nest-boxes may present advantages leading to higher productivity per nesting attempt, such as earlier lay date (Purcell et al. 1997, Czeszczewik 2004, but see Norris et al. 2018), larger clutch size (Robertson and Rendell 1990, Czeszczewik 2004, Norris et al. 2018), lower predation risks (Nilsson 1984, Purcell et al. 1997, Mitrus 2003, but see Czeszczewik 2004), fledging more young (Purcell et al. 1997, Norris et al. 2018) and having higher nesting success (Llambías and Fernández 2009, but see Johnson and Kermott 1994). These patterns appear to vary across species (Robertson and Rendell 1990, Purcell et al. 1997, Mitrus 2003). Nest-box studies have been criticised for creating artificial densities of breeding pairs (Hagvar et al. 1990, Alatalo et al. 1991, Lõhmus and Remm 2005, Camprodon et al. 2008, Cockle et al. 2010), altered nest properties, such as microclimate (Maziarz et al. 2017, Strain et al. 2021, Sudyka et al. 2022a), ectoparasite loads (Wesołowski and Stańska 2001) or predation pressures (Mitrus 2003, Czeszczewik 2004). All these cues can potentially change reproductive strategies: increased breeding density may thus lead to increased intra- and inter-specific competition, increased extra-pair paternity rates (Mayer and Pasinelli 2013) and negative density-dependence of reproductive output (Pöysä and Pöysä 2002). In particular, nest microclimate can affect developmental rates in birds because their reproductive cycle (e.g. oviparity) allows the abiotic conditions to directly act on the development from the earliest embryonic stages. Thus, the changes in the mean or variance of nest temperatures (Sudyka et al. 2022a) may affect fitness in wild populations and induce life-history shifts in the long term (Dawson et al. 2005, Duckworth et al. 2017, Mueller et al. 2019). The impact of nesting microclimate can be mitigated by parental care (e.g. incubation or brooding behaviour (Ospina et al. 2018, Mueller et al. 2019)), but only to a certain extent. For example, nest microclimate can alter parasite loads – due to material accumulation when nest-boxes are not routinely cleaned, as opposed to natural cavities where nesting material usually decomposes naturally over one year (Wesołowski 2000) – or affect the avian gut microbiome (Maraci et al. 2022). Moreover, higher temperatures in nest-boxes may be relevant for reproduction onset because the temperature is a cue for egg-laying (Dhondt and Eyckerman 1979). Additionally, it is hard to generalise many conclusions even within nest-box studies because of major differences in nest-box design and inadequate reporting among studies (Lambrechts et al. 2010). As a result, many authors have argued that for some aspects of the ecology of secondary cavity nesters, data collected from nest-boxes may not provide an accurate representation of trait distribution as encountered in natural populations (Alatalo et al. 1988, Møller 1989, Robertson and Rendell 1990, Purcell et al. 1997, Wesołowski and Stańska 2001, Mitrus 2003, Czeszczewik 2004, Wesołowski 2011). Thus, evolutionary and ecological interpretations of nest-box studies should be collated with observations of birds in

natural cavities. At the bare minimum, potential confounding effects stemming from the differences in nesting parameters from the reference state (natural cavities) should be discussed (Robertson and Rendell 1990, Wesołowski 2011). Unfortunately, this recommendation is not given much consideration, but we need knowledge on whether cavity type (natural versus artificial) creates a bias regarding our inference of life-history and fitness trait distribution. This context brings about a major caveat of all up-to-date studies comparing life-history traits in natural and artificial breeding cavities: nest-boxes are generally set up in secondary forests outside urbanized areas (Nilsson 1984, Alatalo et al. 1988, Rendell and Robertson 1989, Robertson and Rendell 1990, Johnson and Kermott 1994, Purcell et al. 1997, Llambías and Fernández 2009, Norris et al. 2018) apart from two studies in a primaeval forest (Mitrus 2003, Czeszczewik 2004). This severely limits their relevance to extrapolate results in an urban context and consequently address their functional meaning.

In this paper, we report the results of a comparative study on birds nesting in natural cavities and nest-boxes within one habitat – an urban, seminatural forest with superabundant natural cavities. We evaluate nesting cavity-type effects in two small passerines: blue tits (*Cyanistes caeruleus*, hereafter BT) and great tits (*Parus major*, hereafter GT). They compete for the same pool of breeding sites, but their species-specific differences in morphology, physiology and life-history (e.g. body size, clutch size), open a convenient field for inter-specific comparisons. Specifically, we addressed two questions: 1) is the ecology of nest-boxes different from natural cavities, leading to varying effects on reproductive phenology, and 2) do birds from natural cavities and nest-boxes differ in life-history traits (in particular reproductive success)? Owing to varying temperature profiles between natural cavities and nest-boxes (Maziarz et al. 2017, Sudyka et al. 2022a), we predict a shift in phenology to earlier lay dates in nest-boxes, and an altered incubation behaviour with nest-box-breeding birds starting to incubate earlier than in natural cavities (as daily temperature averages and maxima during nest-site choice are higher in nest-boxes than in natural cavities (Sudyka et al. 2022a) or pairs may settle earlier in boxes due to high competition for tree cavities (Purcell et al. 1997, Norris et al. 2018)). We also predict possible species-specific pre- and post-hatching responses to the altered, artificial properties of nest-boxes. Specifically, in nest-boxes, GT should build smaller nests, because available nesting cavity space is smaller in nest-boxes than in natural cavities chosen by GT (Maziarz et al. 2016), which can negatively influence their clutch size (Møller et al. 2014). In terms of post-hatching responses, BT should suffer more pronounced consequences of the unstable thermal conditions in nest-boxes relative to natural cavities (e.g. lower fledgling number and fledging success), because smaller species are more vulnerable to thermoregulatory insults (McKechnie and Wolf 2010). Finally, we also predict that nest-boxes will provide a safer breeding environment than natural cavities in terms of predation rates in both species.

Material and methods

While we focus here on key methodological aspects of the study, we provide extensive information on natural cavity versus nest-box ecology in the Supporting information, such as details on: study species, study plots, nest search and monitoring, pilot season, natural cavities within the nest-box plot, variables for main analyses, environmental data collection and weather conditions, statistical analyses and discussion of year-specific effects.

Briefly, the study was conducted over three consecutive field seasons (2017–2019, with two seasons of comparative study) in Bielany Forest (hornbeam–oak stands with > 100 years succession), located in Warsaw, Poland. Within the forest, two plots were monitored (Fig. 1) – one with only natural cavities (30 ha core area) and one with nest-boxes (15 ha with 65 nest-boxes woodcrete Schwegler 1b, Table 1). The plots' edges were spatially separated by 200 m to avoid non-random cavity type choice by parents due to the inter and intra-specific competition for a particular cavity type if interspersed on the same plot (i.e. different subsets of birds breeding in nest-boxes and natural cavities; see Supporting information). The small distance ascertained that the plots shared the same environmental patch structurally (in terms of tree composition) and as a habitat (in terms of predator pressure and food availability). At the same time, the study design allowed for a random, quality-independent distribution of parents between cavity types. We performed intensive nest searches at the natural cavity plot and weekly nest-box rounds on the nest-box study plot to record lay date, clutch size, incubation start (actual incubation determined by egg candling, allowing precise recognition of the start of embryo development, a technique widely used in the poultry industry adopted for small hole-nesting passerines (Ojanen and Orell 1978)), hatching date, number of hatchlings and fledglings, the exact daily fledging date (after 17 days from hatching we visited nests every day to check for fledging) and any chicks that failed to fledge. If a nesting attempt failed entirely (was deserted, i.e. no chicks fledged), we recorded the stage of desertion and – if possible – its specific reason (Supporting information). To characterize the environmental conditions occurring during the reproductive seasons, we collected data on food availability (frass fall collection, recorded as g m^{-2} day^{-1}) at the study plots, weather (average, minimum and maximum daily ambient temperature, daily sum of precipitation, relative humidity and average daily wind speed), and noise and air pollution (as the study area was located within a capital city, we also tested whether noise and air pollution were uniform across the two plots and did not interfere in our study design; see Supporting information). Nest dimensions in both natural cavities and nest-boxes (Table 1) were measured using a measuring tape (precision 0.1 cm, according to the methodology in Wesołowski and Rowiński (2012) and Maziarz et al. (2016)). In case of high and inaccessible natural cavities, nest height was measured with an altimeter/clinometer (Suunto PM-5/1520) that allows conversion of the measured angle into the absolute height of the object (precision 0.25 m). Depending on natural
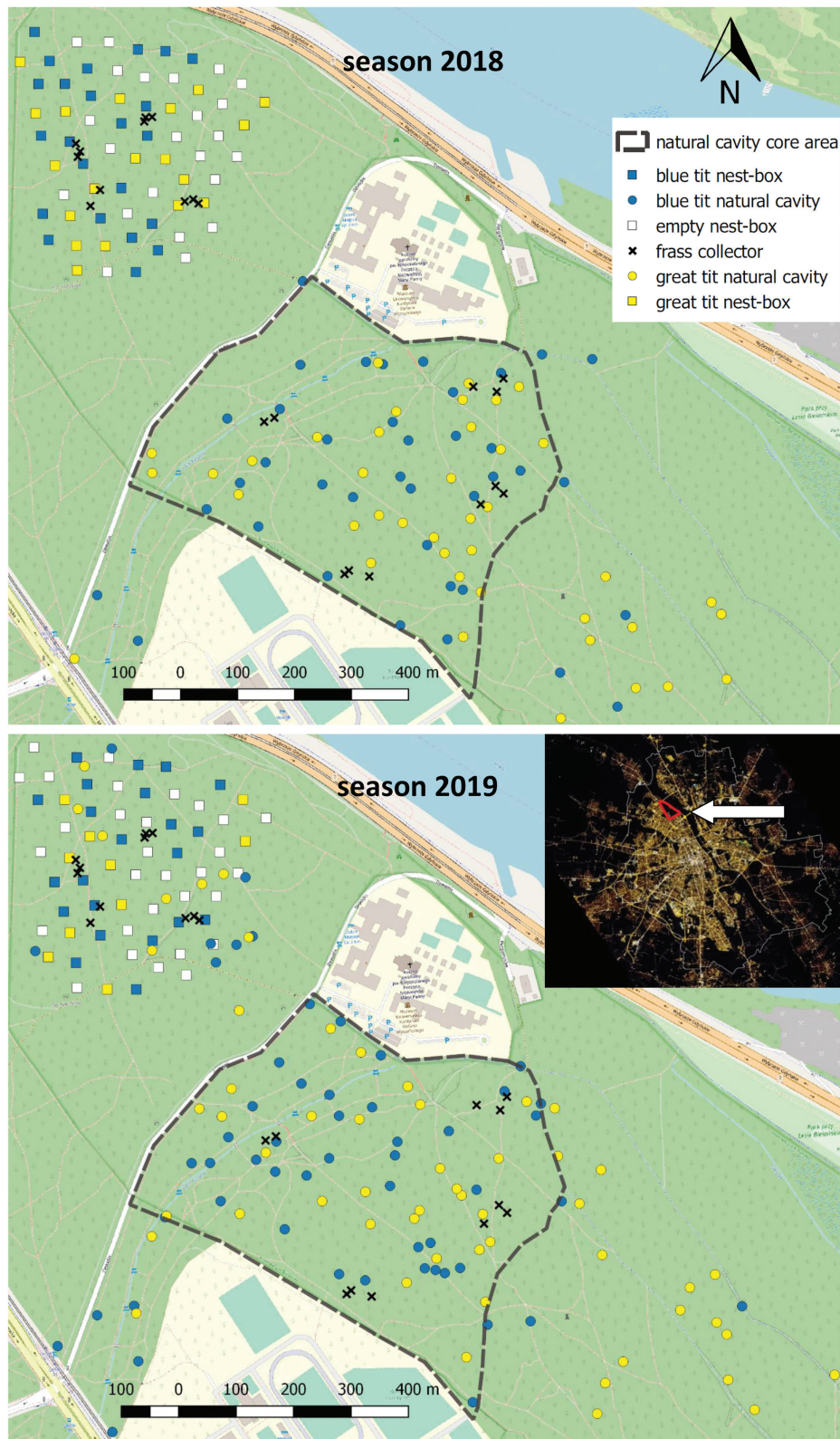
Figure 1. Map of study plots with nest distribution in Bielany Forest in 2018 (top) and 2019 (bottom). The night-time photograph indicates the location of Bielany Forest in the Warsaw city matrix (source: <http://zoz.cbk.waw.pl/>).

Table 1. Basic parameters for Blue tit and Great tit nesting sites in all natural cavities and nest-boxes in two breeding seasons.

| Cavity parameter | Blue tits | | | | | | Great tits | | | | | |
| | Natural cavity | | Nest-box | | U-Mann–Whitney | | Natural cavity | | Nest-box | | U-Mann–Whitney | |
	Median (range)	n	Median (range)	n	U	p	Median (range)	n	Median (range)	n	U	p
Height [m]	7.5 (0.6–17.2)	82	2.9 (2.9–3.0)	46	580.5	**< 0.001**	4.7 (0.3–16.2)	87	2.9 (2.9–3.0)	29	870.0	**0.012**
Height* [m]	4.7 (0.6–12.5)	51	2.9 (2.9–3.0)	46	580.5	**< 0.001**	3.1 (0.3–10.7)	65	2.9 (2.9–3.0)	29	841.0	0.402
Entrance width [cm]	2.5 (1.6–18.5)	45	3.2 (–)	46	621.0	**< 0.001**	3.8 (2.1–9.0)	61	3.2 (–)	29	652.5	**0.041**
Entrance height [cm]	9 (2.5–79.0)	45	3.2 (–)	46	161.0	**< 0.001**	10.2 (3.5–250.0)	61	3.2 (–)	29	0.0	**< 0.001**
Entrance area [cm²]	21.4 (3.5–552.1)	45	8.0 (–)	46	276.0	**< 0.001**	35.3 (9.6–589.0)	61	8.0 (–)	29	0.0	**< 0.001**
Depth [cm]	21.0 (7.2–92.0)	43	9.1 (6.6–10.2)	46	107.0	**< 0.001**	24.0 (0.0–66.0)	58	9.4 (8.1–11.1)	28	186.0	**< 0.001**
Safety distance [cm]	22.2 (7.2–92)	43	9.1 (6.6–10.2)	46	68.5	**< 0.001**	26.0 (8.0–66.0)	58	9.4 (8.1–11.1)	28	100.0	**< 0.001**
Nest length [cm]	10.5 (5.0–22.0)	42	11.4 (–)	46	874.0	0.406	14.8 (8.0–42.0)	58	11.4 (–)	28	308.0	**< 0.001**
Nest width [cm]	11.0 (5.0–24.0)	42	11.4 (–)	46	874.0	0.406	13.2 (4.0–26.5)	58	11.4 (–)	28	336.0	**< 0.001**
Bottom area [cm²]	87.3 (19.6–395.8)	42	102.1 (–)	46	828.0	0.213	160.0 (28.3–651.4)	58	102.1 (–)	28	336.0	**< 0.001**
Volume [cm³]	1883.2 (551.3–15 833.6)	42	923.7 (673.7–1041.1)	46	278.0	**< 0.001**	3502.1 (289.0–41 888.1)	57	959.5 (826.8–1133.0)	28	161.0	**< 0.001**

All measurements were done according to the methodology in Wesołowski and Rowiński (2012) and Maziarz et al. (2016).
Height: measured at the bottom of entrance above ground level, in all cavities including inaccessible ones; Height*: for accessible cavities with known success rate. Subsequent measurements were done only in accessible cavities. Entrance width: largest horizontal dimension; Entrance height: vertical dimension; Entrance area: approximated to an ellipse area = π × 1/2 entrance width × 1/2 entrance height; Depth: distance from entrance to the nest measured vertically; Safety distance: shortest distance from entrance to the nest (often measured diagonally); Nest length: size of nest cup measured from entrance to the opposite wall; Nest width: size of nest cup measured perpendicularly to the nest length; Bottom area: nest size approximated to an ellipse area = π × 1/2 nest width × 1/2 nest length; Volume: nest size approximated to a cylinder volume = bottom area × depth. Significant differences (p < 0.05) marked in bold.

cavity height, nests were reached from the ground with a ladder or using special spikes for climbing. We recorded cavity exposure [entrance facing one of the eight cardinal and intercardinal directions; noted as an important nesting parameter for some species (Rendell and Robertson 1994, Ardia et al. 2006)]. All cavities were marked for coordinates (GPSMAP 64s, Garmin). Maps and area counts were made using QGIS open software ver. 2.18 (QGIS Development Team 2020). We also investigated in detail the microclimate within nests (results published elsewhere: Sudyka et al. 2022a).

Statistical analysis

Details of statistical analyses of environmental variables and breeding densities, nest-box occupancy and desertion rates are presented in the Supporting information. To test for potential differences in life-history and fitness parameters between breeding events occurring in natural cavities and nest-boxes (see Supporting information for the detailed description of all parameters), we used general linear models, introducing cavity type (natural cavity versus nest-box), year and their interaction as explanatory variables. When non-significant, the interaction was removed. We accounted for the lay date (fitted as a linear and quadratic term) in all analyses (introducing it as a continuous covariate) but retained it as either linear or quadratic effect only if significant (and improving model fit using AIC-χ^2 comparing models) as the main term or in interaction. We checked all models for overdispersion and multicollinearity (first, we checked the correlation of all studied variables and supplemented this analysis with calculating variance inflation factor scores in all models, but these never exceed 5). We used Gaussian distribution for normally distributed data (lay date, clutch size, incubation start, hatching and fledging dates, number of fledglings and nesting time), binomial distribution to test success measured in binary outcomes (hatch rate, defined for all nests with at least one egg laid, whereas hatching success concerned only the nests that managed to hatch) or proportion of successful cases (hatching success weighted by clutch size, fledging success weighted by hatchling number). In the case of fledging success, we observed overdispersion; thus we introduced quasibinomial distribution to achieve optimal model fit. We performed Z-score scaling of all continuous variables for clarity of parameter estimates. Basic nest dimensions of natural cavities and nest-boxes were compared with U Mann–Whitney tests (Table 1). All analyses were performed in R (ver. 4.0.4) (<www.r-project.org>).

Results

Environmental variables were uniform between plots; 2019 was an unfavourable year in comparison to 2018, with less food, and colder and more humid weather

All measured environmental variables were highly homogeneous between the natural cavity and the nest-box plots (Supporting information). At the same time, temporal

variation was recorded for these variables independently of plot location. Food availability was uniform between the natural cavity and nest-box plots ($\chi^2 = 0.992$, $p = 0.319$). However, it was lower in 2019, and the timing of peak food availability differed between years, with a high peak of caterpillars occurring already in the first week of May in 2018, and a much lower peak recorded in the fourth week of May in 2019 (significant year effect and year × sampling event interaction, Supporting information). Weather patterns were significantly different between years, with 2019 being unfavourable in terms of temperature, humidity and precipitation (see weather data in Supporting information). Consequently, 'year' was always kept as a fixed factor in our analyses.

Breeding densities in natural cavity and nest-box plots were high

The number of breeding BT and GT observed in the natural cavity plot and in the nest-box plot was of the same order of magnitude, yet overall was lower in the natural cavity plot. In 2018, we observed 10.3 pairs of BT and 10.0 pairs of GT/10 ha in the natural cavity plot and 15.3 pairs of BT and 12.7 pairs of GT/10 ha in the nest-box plot. In 2019, we additionally performed systematic searches of cavities in nest-box proximity (in the nest-box plot), and we observed 20.0 pairs of BT (15.3 in boxes and 4.7 in cavities) and 12.0 pairs of GT (6.7 in boxes and 5.3 in cavities)/10 ha. In the natural cavity plot we recorded 13.3 pairs of BT and 10.0 pairs of GT/10 ha. The overall proportions of BT versus GT nests (without natural cavities at the nest-box plot in 2019) did not differ between natural cavities and nest-boxes, although there was a tendency for fewer GT (25% of the total number of nests) than BT (35%) in nest-boxes ($\chi^2 = 2.847$, $df = 1$, $p = 0.092$). The proportion of species in both types of cavities (natural versus nest-boxes) did not differ between years ($\chi^2 = 0.542$, $df = 1$, $p = 0.462$).

In 2019, fewer nest-boxes were occupied than in 2018 (56.9 versus 75.4% nest-box occupancy by tits) and the occupancy was not affected by nest-box exposure (Supporting information). The proportion of species in occupied nest-boxes did not differ between years ($\chi^2 = 1.491$, $df = 1$, $p = 0.222$), with more BT than GT each year (Supporting information).

Overall nest desertion rate did not differ, but its causes varied between cavity types

We were able to determine nesting outcome (success, that is, if at least one chick fledged) in 202 nests (97 BT, 94 GT and 11 tit nests that were deserted before the species could be assigned). We also identified 59 nests – 23 GT and 36 BT – in natural cavities, but these were inaccessible, thus we did not record their outcome. There were no differences in overall desertion rate between the cavity types (36 out of 116 initially occupied natural cavities (31.0%) versus 27 out of 86 initially occupied nest-boxes (31.4%, $\chi^2 = 0.537$, $p = 0.464$, Supporting information)); however, in 2019 there were more desertions than in 2018 (40 out of 101 (39.6%) versus 23 out

of 101 (22.8%) nesting attempts). Cavity exposure did not influence the desertion rate (Supporting information). The analysis of reasons/stages at which the desertions occurred showed differences between cavity types ($\chi^2 = 12.014$, $p = 0.017$, Supporting information): in natural cavities, we observed a higher occurrence of whole clutch predation (7.8% versus 2.3% of all nests) and instances of collapsing and soaking (3.5% versus 0%), while in nest-boxes desertions after hatching (without specific reasons) were more frequent (5.8% versus 1.7%). In both types of cavities, the greatest number of nest desertions occurred at early breeding stages (desertions other than predation or collapsing): specifically, at the nest building stage for nest-boxes (12.8% of all nests) and at the egg-laying/incubation stage in natural cavities (12.2% of all nests). Differences in stages/reasons of desertions were not significant across years, but they varied between cavity types in the two study seasons (significant nest type × year interaction, Supporting information and Fig. 2).

Phenology. From egg-laying till fledging: similar egg laying and hatching dates, accelerated incubation start and later fledging in nest-boxes

In both species, lay dates did not differ between natural cavities and nest-boxes (Fig. 3A, B, Table 2) but were earlier in 2019 in BT. Importantly, both BT and GT in nest-boxes accelerated incubation start compared to natural cavities (Fig. 3C, D, Table 2). In BT, there was a negative quadratic effect of the lay date on incubation start: early and late clutches delayed incubation, irrespective of the type of cavity they bred in (Supporting information). In GT, the incubation start was also delayed in the unfavourable year of 2019 relative to the favourable year 2018. Interestingly, GT accelerated incubation with later laying dates only in nest-boxes, but the lay date did not affect incubation start in natural cavities (significant interaction lay date × cavity type, Supporting information).

For both BT and GT, the hatching date was not affected by cavity type, but BT fledged later in nest-boxes than in natural cavities (Fig. 4A, mean number of days from 1 April ± SD: 57.9 ± 7.46 versus 56.5 ± 3.83, respectively, Table 2) and later in 2019. No such relations were observed in GT, and the fledging date was uniform between cavity types (Fig. 4B, nest-boxes: 57.0 ± 3.19, natural cavities: 58.2 ± 3.23, Table 2) and between years.

Reproductive success: BT produced fewer nestlings and had lower hatching and fledging success in nest-boxes

In BT, there was a tendency for larger clutch size in nest-boxes, but the effect was only significant in interaction with year: in the favourable 2018, there were more eggs in nest-boxes than in natural cavities (Table 2). However, no such differences were observed in the adverse year 2019. The number of eggs laid by GT was not different between natural cavities and nest-boxes, but they laid fewer eggs in 2019.

Hatch rate (the ratio of nests with successfully hatched eggs to all nests with at least one egg laid) in BT did not differ depending on cavity type but tended to be lower in the year with poorer weather (2019). Interestingly, the BT hatch rate decreased later in the season (with increasing lay date) only in natural cavities but not in nest-boxes (interaction lay date × cavity type, see Supporting information). In GT, the hatch rate was uniform between cavity types and years but, just like in BT, it decreased later in the season in natural cavities and increased in nest-boxes (Supporting information).

BT hatching success (the proportion of eggs that hatched within a clutch, calculated only for nests that successfully hatched at least one chick, i.e. for a later nesting stage than the hatch rate) was lower in nest-boxes than in natural cavities, though this result was year-dependent (Table 2). This effect stems from the significant interaction cavity type × year: in natural cavities, hatching success was similar in both years, while only in nest-boxes was it lower in 2018 (clutch size in that year was larger in nest-boxes than in natural cavities: BT laid more eggs but many failed to hatch). In GT, hatching success was stable across cavity types and years, but the significant interaction shows an opposite direction to what was reported for BT: hatching success was lower in nest-boxes than in natural cavities only in the adverse 2019 year.

BT produced fewer fledglings while nesting in nest-boxes than in natural cavities (Fig. 5A, mean ± SD: 6.1 ± 3.70 versus 7.1 ± 2.74, respectively; Table 2). Interestingly, for GT, the opposite trend was observed, as GT tended to raise more fledglings in nest-boxes, although this association was not significant (Fig. 5B, 7.0 ± 2.73 versus 5.8 ± 3.18, Table 2). The number of fledglings was lower in the adverse 2019 in both species.

Fledging success (the proportion of chicks fledged to hatchling number per nest, calculated only for nests that successfully hatched at least one chick) in BT was lower in

nest-boxes relative to natural cavities and in 2019 (Table 2). In GT, neither type of cavity nor year influenced fledging success.

Nesting time (the number of days from hatching till fledging) was longer for BT in nest-boxes when compared to natural cavities (Fig. 4C, mean ± SD: 19.9 ± 0.92 versus 19.2 ± 1.07, respectively, Table 2); while in GT, there was only a tendency for longer nesting time in nest-boxes (Fig. 4D, 19.5 ± 1.22 versus 18.4 ± 1.54, respectively, Table 2). The significant interaction year × lay date in GT shows that, in the adverse year 2019, nesting time got shorter later in the season; while in 2018, nesting time increased later in the season (Supporting information). Nesting time was uniform between years for both species.

Nest dimensions: no correlation with phenology or fitness proxies

For nesting, tits used natural cavities formed mainly in hornbeams *Carpinus betulus* and oaks *Quercus robur* (Supporting information). Natural cavities of both species were situated higher above ground level than nest-boxes (Table 1 for all cavity dimensions and test results). Importantly, however, in GT, the average height of accessible natural cavities with known nesting outcomes was no different to nest-box height. The entrance holes of nest-boxes were wider than in natural cavities for BT breeding events but narrower in the case of GT. The entrance hole height (vertical dimension) was consistently lower in nest-boxes. In both species, nests in natural cavities were located much deeper, and safety distance – the shortest distance from the entrance to the nest, an important protection against predation – was greater than in nest-boxes, particularly in GT, which have deeper nests than BT. The nest bottom area (nest cup size) was larger in natural cavities of GT but not of BT.
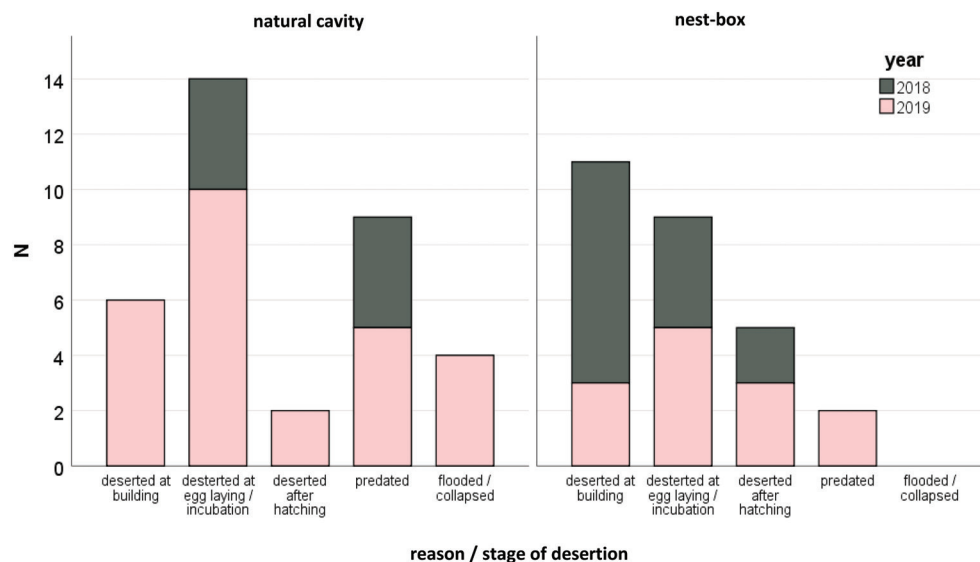

Figure 2. Reasons for/stages of nest desertions in natural cavities (left) and nest-boxes (right). Data from 86 nest-boxes (2018: 49, 2019: 37) and 115 natural cavities (2018: 51, one case where female incubated an empty nest was excluded, 2019: 64). Bars show number of cases.
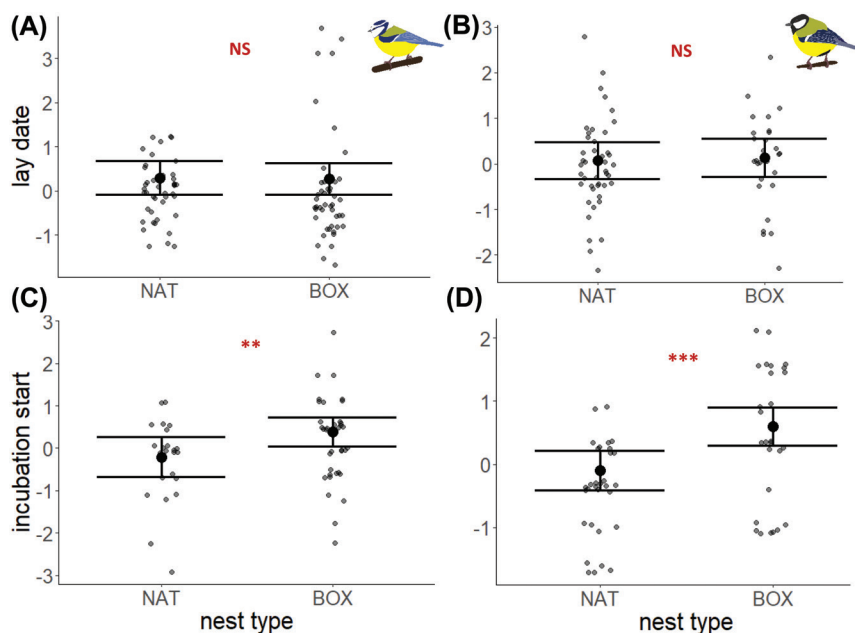
Figure 3. Lay date (A), (B) and incubation start (C), (D) of blue tits (A), (C) and great tits (B), (D) breeding in natural cavities (NAT) and nest-boxes (BOX) in Bielany Forest. Predicted values ± 95% CI are shown on Z-score scaled response variables in days. Significance levels for cavity type: NS: not significant, **: $0.001 < p < 0.01$, ***: $p < 0.001$.

In natural cavities, there was no correlation between nest size (bottom area) and clutch size in BT ($r = 0.197$, $p = 0.296$, $n = 30$) and GT ($r = 0.124$, $p = 0.459$, $n = 38$) or number of fledged young in BT ($r = -0.056$, $p = 0.766$, n = 31) and GT ($r = 0.119$, $p = 0.457$, $n = 41$). We also tested height above ground and bottom area as separate covariates in our main models (Table 2) and in the model on nesting desertions (Supporting information), but these invariably and in both species did not impact lay date, clutch size, number of fledglings, fledging success, nesting time and nest desertions (all $p > 0.05$). As such, they were removed from final models.

Discussion

This is the first study to compare the fitness consequences of breeding in artificial nesting cavities as opposed to natural cavities in an urban setting. More generally, this is also one of the few studies explicitly testing differences in passerine life-history traits and fitness variation inferred from natural cavities and nest-boxes in a quasi-experimental setting. We demonstrate that cavity-type – man-made or natural – can affect breeding performance in a species-dependent way. In comparison to natural cavities, BT in nest-boxes had lower hatching and fledging success and, in consequence, fledged fewer young (Fig. 5A). BT chicks from nest-boxes also spent more time in the nest (Fig. 4C, nesting time: from hatching till fledging) and fledged later in the season (Fig. 4A) than birds nesting in natural cavities. In GT, differences in breeding parameters between natural cavities and nest-boxes were not apparent (Fig. 3 and 4). Their reproductive success was similar or tended to be superior in

nest-boxes than in natural cavities (e.g. a tendency for higher fledgling number, Fig. 5B). Notably, both species experienced shifts in the onset of natural incubation as they were found to start incubating earlier in nest-boxes, often before clutch completion (Fig. 3C, D), which can lead to increased hatching asynchrony (Stenning 1996).

Breeding density and reproductive success

Breeding densities were very high in both the natural cavity plot (more than 10 pairs/10 ha for both species), and even more so in the nest-box plot (more than 12 pairs/10 ha for both species). Specifically, these values ranged as follows for the two species: in natural cavities BT 10.3–13.3 and GT 10.0–10.0 (pairs/10 ha); in nest-boxes BT 15.3–20.0 and GT 12.0–12.7 (pairs/10 ha). These appear higher than densities across eight other nest-box sites in Warsaw and its vicinity in the two study years, mean ± SD/10 ha: 5.6 ± 4.4 BT and 7.2 ± 3.3 GT; unpubl.). The average density in an oak–hornbeam–lime forest patch in Białowieża National Park (treated as a baseline primaeval ecosystem for breeding densities) is 4.0 pairs/10 ha for BT and 4.9 pairs/10 ha for GT (Wesołowski et al. 2010). Other urban habitats have breeding densities of the same order of magnitude as observed in our study: in several urban and rural habitats of southern Finland (mean ± SD/10 ha: 5.2 ± 0.9 for BT, 17.3 ± 1.8 for GT; Solonen 2001). This suggests that tit breeding densities are not necessarily driven by the availability of natural cavities (which are in surplus in both the primaeval forest and in our urban site). Instead, they are likely to be the result of other ecosystem attributes and dynamics, which undoubtedly deserve further work.

Table 2. Results of final general linear models of life-history and fitness variation in natural cavities and nest-boxes in the two study years (favourable 2018 and adverse 2019) in Bielany Forest. Interactions of the two main factors are retained and presented only if significant. Natural cavity and year 2018 are the reference values for the estimates. All estimates are shown after Z-score scaling of continuous variables. All models also accounted for lay date (estimates in the Supporting information), but these were retained only if significant (as a main factor or in interaction). Estimates for significant factors ($p < 0.05$) are indicated in bold, trends ($p < 0.20$) in italics. Sample sizes for each analysis are shown in the Supporting information.

| | Blue tits | | | | | | Great tits | | | | | |
| | Cavity type | | Year | | Cavity type × year | | Cavity type | | Year | | Cavity type × year | |
Nest data	Estimate ± SE	Pr(> χ²)	Estimate ± SE	Pr(> χ²)	Estimate ± SE	Pr(> χ²)	Estimate ± SE	Pr(> χ²)	Estimate ± SE	Pr(> χ²)	Estimate ± SE	Pr(> χ²)
Lay date	−0.018 ± 0.209	0.933	**−0.521 ± 0.209**	**0.013**		NS	0.065 ± 0.248	0.793	−0.197 ± 0.242	0.416		NS
Clutch size	*0.842 ± 0.268*	*0.140*	0.382 ± 0.282	0.264	**−1.121 ± 0.378**	**0.003**	−0.167 ± 0.244	0.493	**−0.633 ± 0.240**	**0.008**		NS
Incubation start	**0.598 ± 0.229**	**0.009**	−0.308 ± 0.253	0.224		NS	**0.700 ± 0.186**	**< 0.001**	**−0.610 ± 0.188**	**0.001**		NS
Hatch rate	*0.402 ± 0.663*	*0.279*	*−1.061 ± 0.672*	*0.102*		NS	1.915 ± 1.556	0.365	0.260 ± 0.811	0.748		NS
Hatching success	**−2.351 ± 1.026**	**0.013**	**−1.008 ± 1.107**	**0.007**	**2.260 ± 1.180**	**0.027**	0.750 ± 0.638	0.373	0.746 ± 0.702	0.222	**−2.277 ± 0.935**	**0.011**
Hatching date	0.049 ± 0.065	0.448	**0.194 ± 0.067**	**0.004**		NS	*−0.136 ± 0.098*	*0.168*	**−0.209 ± 0.107**	**0.050**		NS
Fledgling number	**−0.442 ± 0.220**	**0.044**	**−0.816 ± 0.220**	**< 0.001**		NS	*0.329 ± 0.246*	*0.182*	**−0.506 ± 0.241**	**0.036**		NS
Fledging success	**−0.983 ± 0.480**	**0.034**	**−1.803 ± 0.473**	**< 0.001**		NS	0.106 ± 0.512	0.836	0.373 ± 0.579	0.515		NS
Fledging date	**0.170 ± 0.082**	**0.037**	**0.247 ± 0.084**	**0.003**		NS	−0.016 ± 0.157	0.918	−0.039 ± 0.170	0.821		NS
Nesting time	**0.717 ± 0.242**	**0.003**	0.224 ± 0.242	0.354		NS	0.345 ± 0.268	0.198	0.269 ± 0.283	0.299		NS

Our results indicate that urban BT were more sensitive to artificial nesting cavities than GT. The deterioration in fledging success and fledging number (Fig. 5A), which are key parameters directly related to fitness, shows that nest-boxes may not be optimal breeding places for BT but are completely sufficient for GT. The latter result complements earlier studies comparing the reproductive output stemming from natural cavities and nest-boxes. In tree swallows *Tachycineta bicolor*, nest-boxes were even more productive in terms of fledglings than natural cavities, which was a direct by-product of larger clutch size in the nest-boxes (Norris et al. 2018). Similarly to other studies, we detected no differences in clutch size between natural cavities and nest-boxes (Llambías and Fernández 2009, but see Robertson and Rendell 1990, Czeszczewik 2004). It is often found that clutch size correlates with nest size across species (Møller et al. 2014); however, such correlation was confirmed only in GT (Maziarz et al. 2016) and not in BT (Wesołowski and Rowiński 2012). Likewise, our study did not confirm this relationship and the differences in nest size between cavity types were noted only for GT and not BT (Table 1). Our study reports no overall differences in clutch size and hatching rates between cavity types (i.e. pre-hatching investment, Table 2). As such, the observed effects on fledgling number and success may stem from post-hatching effects (and include differential hatching success that was detected between natural cavities and nest-boxes in BT), related either to cavity properties or investment of parents. We were not able to detect the influence of cavity dimensions (Table 1) on various fitness outcomes. Nor did we record parental investment (provisioning rates or brooding behaviour) between the two types of cavities. Thus, we are not able to exclude such differential investment according to cavity type. The detected post-hatching effects in BT may also have been generated by slightly higher overall breeding densities in the nest-box plot leading to increased competition for food. The rise in density occurs in most studies introducing nest-boxes (Newton 1994b). However, increased density is not always linked with altered interspecific competition (Brawn et al. 1987), and in many species nesting site shortage is more limiting than food availability, meaning that a given area can support the number of breeders increased by nest-box presence (Newton 1994a). The competition explanation is also less plausible based on the specific values reported in this study for natural cavities within the nest-box plot (Supporting information), where birds form natural cavities and nest-boxes experience equal breeding densities and still appear to differ in nestling performance (yet the sample sizes of these data do not allow this to be tested in detail). In absolute values, breeding density variation between the study plots is also limited compared to differences with breeding densities reported in other studies (above). Additionally, year-dependent density variation is consistent between plots, which points to the role of environmental factors for the number of breeding pairs. Nevertheless, the densities we observed are already high, so we cannot exclude that an even slight increase in breeding density can enhance competition for food, also irrespective of the year-specific effects. However, this can only be determined by a
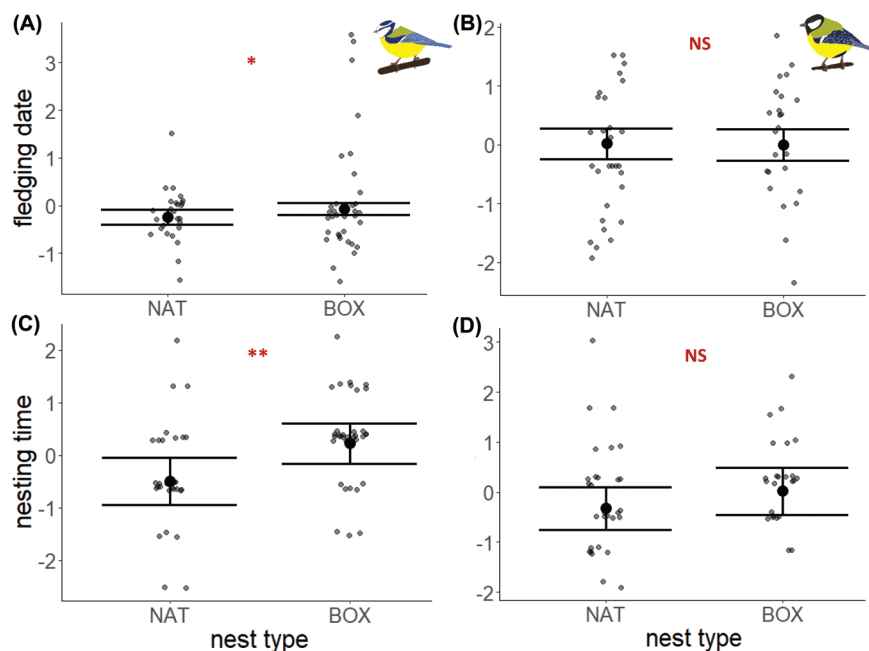
Figure 4. Fledging date (A), (B) and nesting time (the number of days from hatching till fledging; (C), (D) of blue tits (A), (C) and great tits (B), (D) breeding in natural cavities (NAT) and nest-boxes (BOX) in Bielany Forest. Predicted values ± 95% CI are shown on Z-score scaled response variables in days. Significance levels for cavity type: NS: not significant, *: 0.01 < p < 0.05, **: 0.001 < p < 0.01.

direct quantification of inter- and intra-specific competition, for example food base usage in natural cavities and nest-boxes via feeding rates and prey quality, if this explanation holds. Based on the evidence collected, we argue that the most likely explanation of the patterns observed should be attributed to the qualities of each cavity-type per se. Specifically, our data on microclimate indicate that the very apparent differences in cavity properties may underlie the observed differences in fitness outcomes between the two species. During late nesting stages, the maximum daily temperature inside the cavity space was on average 7.4°C higher in nest-boxes and only 1.0°C higher in natural cavities relative to outside temperatures (maximum: 33.5°C, average daily maximum ± SD: 26.7 ± 3.15°C in nest-boxes and 29.8°C and 20.6 ± 3.94°C in natural cavities). Maximum and average daily humidity

were also higher in nest-boxes than in natural cavities (Sudyka et al. 2022a). Moreover, the nesting birds were subjected to even higher temperatures than the values reported within the cavity space, because of the additional heat produced and transferred by thermoregulating siblings (Webb and King 1983). While still below critical thresholds (McKechnie and Wolf 2010), such conditions can potentially increase the costs of thermoregulation and thus entail biological consequences for nestling development and fitness. Consequently, BT are likely to pay higher costs of such a thermal environment than GT, because evaporative water cooling is more compromised in small birds as their water reserves are smaller (McKechnie and Wolf 2010; before fledging, the studied BT nestlings are 1.4 times smaller in terms of body mass than GT). Moreover, tolerance to high temperatures decreases with brood size
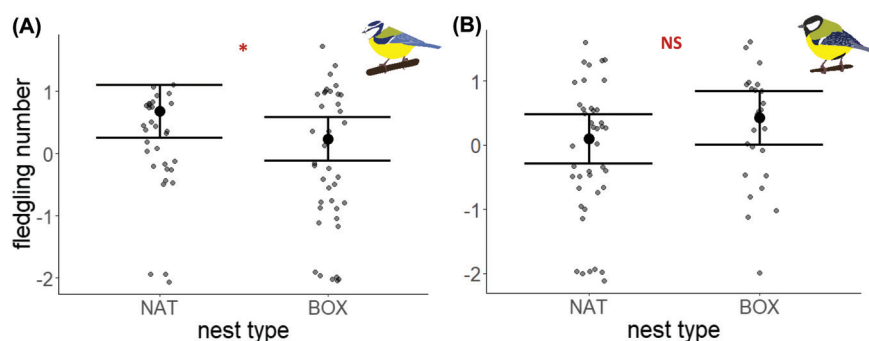

Figure 5. Number of fledged young of blue tits (A) and great tits (B) breeding in natural cavities (NAT) and nest-boxes (BOX) in Bielany Forest. Predicted values ± 95% CI are shown on a Z-score scaled response variable. Significance levels for cavity type: NS: not significant, *: 0.01 < p < 0.05.

(Mertens 1977), possibly explaining the lower resistance to microclimate deterioration in BT as they are known to have larger clutches than GT.

Worse reproductive outcomes may also be recorded in species which are poor competitors for (or have a preference towards) a particular cavity type (Norris et al. 2018). In accordance with this prediction, some studies suggested natural cavity preference in BT and nest-box preference in GT, although these conclusions are based on small sample sizes (Lõhmus and Remm 2005). It is also possible that the choice of cavity type might be personality-dependent, primarily due to neophobic reactions to freshly installed nest-boxes. However, nest-boxes were set up four months prior to the 2018 breeding season and, as such, were not entirely novel in the birds' breeding environment. Usually, neophobic reactions occur and are studied on a shorter time scale of days or even hours (Batisteli et al. 2022). Our data do not allow us to formally test the preference of nest-boxes over natural cavities in either species but, unlike in the case of collared flycatchers *Ficedula albicollis* which bred only in nest-boxes when provided and avoided natural cavities (Mitrus 2003), there is no apparent evidence for greater preference or avoidance of nest-boxes in either species. BT and GT bred in both types of cavities if available in the same plot (although, if interspersed, parents in each cavity type appear to vary in investment in clutch size, chick body mass and condition or overall success rate; see Supporting information). Owing to the slight study plot separation in space, it is unlikely that the differences observed in bird fitness between natural cavities and nest-boxes stem from varying individual quality between parents using the two types of cavities. Birds in our study came from the same population, and they did not need to compete for the two types of cavities in the same plot as these were spatially distinct (Fig. 1). In Bielany Forest, the nest-boxes were newly introduced at the beginning of 2018, and there was thus no possibility of establishing specific phenotypes related to the nesting place type in such a short time (for example, via preference to breed in the same type of cavity in which a bird was raised). Importantly, we did not detect any major differences in basic phenotypic parameters (age, body size and mass, promiscuity, parasite load or colouration) in BT or GT parents from natural cavities versus nest-boxes (Janas et al. 2022, Di Lecce et al. unpubl.).

Phenology

We detected later fledging dates (Fig. 4A) and longer time spent in nest-boxes relative to natural cavities in BT (Fig. 4C) and a similar yet non-significant trend in GT (Fig. 4D). The optimal time to fledge is likely determined by the rates of mortality inside the nest as opposed to those outside of it (Martin et al. 2018). In our study setup, the pressure experienced inside the nest differed depending on cavity type: predation was lower in nest-boxes (Fig. 2, Supporting information), similar to other comparative works (Nilsson 1984, Purcell et al. 1997, Mitrus 2003). At the same time, outside (extrinsic) mortality rates should be independent of cavity type because, after fledging, all birds share the same environment (however, this can be altered by slight temporal shifts in fledging date between cavity types in BT). Thus, staying longer can be optimal in a safer nest-box environment. The longer nesting may allow for greater wing development, leading to superior flight performance and increased post-fledgling survival of nest-box fledglings (Lloyd and Martin 2016, Martin et al. 2018). Alternatively, greater temperature amplitudes experienced by the young in nest-boxes (Strain et al. 2021, Sudyka et al. 2022a) can create a physiological and metabolic challenge; thus resources normally allocated to growth and development may have to be traded-off with the increased need to thermoregulate. In any case, such delay in fledging may also hamper BT fitness: birds that fledge later have worse lifetime reproductive success after recruitment (Visser and Verboven 1999), and a lower probability of survival (Perrins 1965, Cooke et al. 1984, Naef-Daenzer et al. 2001), and produce fewer recruits into the breeding population (Naef-Daenzer et al. 2001, but see Monrós et al. 2002).

For the first time, we show that cavity type is an important cue for incubation onset. Both species accelerated incubation start while breeding in nest-boxes. This could lead to larger hatching asynchrony and mortality of the youngest chicks (Stenning 1996). Interestingly, GT accelerated incubation with later laying dates only in nest-boxes, but the lay date did not affect incubation behaviour in natural cavities, possibly because temperature and humidity are stable throughout the breeding season in natural cavities (Sudyka et al. 2022a). Such phenological shift is yet another factor that could influence reproductive outcomes of tits breeding in nest-boxes.

Nest desertions

We did not detect differences in overall nest desertion rates between the two types of cavities. In natural cavities, height above the ground may be important for nesting failures (Rendell and Robertson 1989, Alatalo et al. 1991), but it was not correlated with the desertions identified in our study. In primaeval habitats (such as Białowieża National Park), higher-situated nests are more prone to losses due to the presence of specialized predators, e.g. dormice (Maziarz et al. 2016), which are absent in most secondary and urban forests. In our study, some of the highest natural cavities were not always accessible (Table 1), yet we still detected higher predation in natural cavities compared to nest-boxes. However, we showed that the reasons for desertions differed between the types of cavities (Supporting information, Fig. 2): nest-boxes were frequently abandoned at building, which could be explained by their unstable microclimate. Indeed, artificial cavities get warmer during daytime (a cue for building onset) but cool down rapidly at night (a signal to discontinue nest building), whereas cavities are thermally stable also at this early nesting stage (Maziarz et al. 2017, Sudyka et al. 2022a). Similarly to other studies comparing natural cavities and nest-boxes (Wesołowski 2011), we observed higher nest soaking in natural cavities, which is related to the construction of nest-boxes (e.g. stable roofs). Overall predation

rates were low, probably because of the paucity of natural predators in Bielany Forest and close human presence (especially when compared to Białowieża National Park predation rates (Wesołowski and Rowiński 2012, Maziarz et al. 2016)). However, they were lower still in nest-boxes (relative to natural cavities), which is in accordance with previous work (Nilsson 1984, Møller 1989, Purcell et al. 1997, Mitrus 2003, Llambías and Fernández 2009). Nevertheless, the predation rate appears to be year-dependent, since in the natural cavity plot during the 2017 pilot season, it was three times higher than in the remaining two seasons, exceeding 21% (see Supporting information). Nest-boxes appear to be safer, although nest depth and safety distance are greater in cavities (Table 1). Predators may have difficult access to nest-boxes because these have holes with a smaller vertical dimension and are narrower (in the case of GT) compared to natural cavities, which may suffice as protection in the type of habitat with relatively low predation pressure. However, entrance hole size does not necessarily influence overall nest predation rates in areas with high predation risks (Wesołowski 2002). We cannot exclude the possibility that the pattern of nest-boxes being safer may change over time and that they can possibly become an ecological trap by providing a source of easy food for quickly adapting predators (Hagvar et al. 1990), also typically encountered in urban environments, such as cats or corvids.

Conclusions and outlook on the ecological importance of old-growth tree stands

The results of our study indicate that nest-boxes may turn out to be an ecological trap for some species. In BT, the most important fitness proxies that could be inferred in both cavity types (e.g. fledging success, fledgling numbers, time spent in the nest and fledging date) were sensitive to cavity type and resulted in lower values in nest-boxes. At the same time, GT performance appeared not to be affected by cavity type (except for shifts in incubation patterns, which ultimately did not result in differential fitness outcomes). This strengthens the knowledge of species-specific effects of the introduction of man-made cavities that may benefit one species over another (Duckworth et al. 2017). However, the results we provide have to be taken with caution as they were gathered only across two study seasons. Studies encompassing more seasons are warranted, preferably in a long-term framework, lasting several decades. Data on survival, lifetime reproductive success and recruitment rate of fledglings into the breeding population from the two types of cavities are also needed to determine whether nest-boxes act as an ecological trap in the long run. Nevertheless, our results imply that we have to agree with other authors criticising the unconditional extrapolation of evolutionary and ecological interpretations of nest-box studies to general populations (Robertson and Rendell 1990, Wesołowski 2011). This is particularly true in areas where the availability of natural cavities is likely to outnumber the contribution of nest-boxes at the population level. Within the urban space, places such as cemeteries and large urban parks, especially with snags present (standing, dead or dying trees; Blewett and Marzluff 2005), can upkeep the biodiversity of nest excavators such as woodpeckers (Bovyn et al. 2019, Smith and Minor 2019), and consequently maintain the pool of natural cavity sites. Importantly, it has been demonstrated that it is the suitability of natural cavities, rather than their abundance, that determines secondary hole-nesting bird numbers in managed forests; in the study of Camprodon et al. (2008), a shortage of suitable cavities stemmed from a lack of trees of large diameter. It is also known that to prevent the loss of native species, keeping stable habitat patches greater than 50 ha and increasing their number is vital (Beninde et al. 2015). Therefore, large old-growth stands, such as Bielany Forest, within urbanised areas and beyond are of great importance for cavity-nesting birds (and other non-avian taxa using them). At the same time, nest-boxes can be a valuable source of nesting sites in areas with no natural cavities, including urban areas. Our study may motivate the direct comparisons of breeding performance in other taxa of urban animals in human-provided and natural nesting shelters. Only such knowledge can warrant generalizations about their reproductive ecology.

Author contributions

Joanna Sudyka: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Supervision (lead); Writing – original draft (lead); Writing – review and editing (lead). **Irene Di Lecce**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Lucyna Wojas**: Conceptualization (supporting); Data

curation (supporting); Investigation (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Patryk Rowiński**: Conceptualization (supporting); Data curation (supporting); Investigation (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Marta Szulkin**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent peer review

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Data availability statement

Data are available from Dryad Digital Repository: <https://doi.org/10.5061/dryad.w0vt4b8sb> (Sudyka et al. 2022b).

Supporting information

The Supporting information associated with this article is available with the online version.

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