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

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Short title: Nest-boxes vs natural-cavities in cities

Abstract

To mitigate the shortage of natural breeding sites in cities, nest-boxes are provided for cavity-nesters. However, these are not the breeding sites these animals originally evolved in and optimised their breeding performance to. It thus remains inconclusive if nest-boxes can provide adequate substitutes, ensuring equivalent fitness returns for breeding animals. Additionally, the majority of knowledge on the ecology of urban birds comes from nest-box populations, but no study to date directly compared fitness consequences of breeding inside nest-boxes in relation to natural-cavities in an urban context. This limits our understanding of the urban ecology of cavity-nesters and addressing its functional meaning. We investigate fitness consequences and life-history trait variation according to the nesting site type to provide a comprehensive understanding of conservation potential of nest-boxes in cities and to support/question generalisations stemming from nest-box studies on urbanization. We directly compare the reproductive performance of two small passerines, blue tits and great tits, breeding in nest-boxes as opposed to natural-cavities in a seminatural forest of a capital city using a quasi-experimental setting. We show that the effects of nest 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 nest and later fledging date in comparison to natural-cavities), while great tit performance appeared to be unaffected by nest type. We detected that both species breeding in nest-boxes accelerated incubation onset, but since there were no major differences in pre-hatching traits (lay date, clutch size, hatching rates) between the nest types, we attribute the fitness deterioration to post-hatching effects. Interestingly, overall breeding density of tits in urban natural-cavities was higher than observed in a primeval habitat. Nest-boxes may become an ecological trap for some species and the unaffected species can consequently outcompete them, decreasing overall biodiversity in cities. We highlight the ecological importance of old-growth tree stands, providing natural tree cavities for city-breeding animals. Due to the detected nest 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.

1. Introduction

Natural-cavities can be formed by wood decomposition and/or breaking followed by colonisation by microorganisms, 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). Because of low numbers, or even lack of old-growth tree stands in which natural decomposition takes place, and a lower number of active excavators (Tomasevic & Marzluff, 2017), most urban areas (except old parks) present less natural nesting sites for cavity-nesting birds (Blewett & Marzluff, 2005; LaMontagne et al., 2015). In consequence, these birds in cities use a variety of artificial cavities such as lamp posts, mailboxes, ashtrays, cavities in bridges or any place providing appropriately narrow entrance and space to build a nest (Bańbura & Bańbura, 2012; Valera et al., 2019). However, such places are very unstable and can easily be overheated or flooded; as a result less young fledge (Lesiński, 2000). In many cities, nest-boxes are offered as a conservation measure to increase breeding opportunities for birds, and are perceived as human facilitation - a positive interaction to promote species diversity (Hacker & Gaines, 1997; Tomasevic & Marzluff, 2017). In some cases this is beneficial, increasing breeding probability (Sumasgutner et al., 2020), but on the other hand increasing local densities may boost competition among birds using the same type of nest (Diamond & Ross, 2019; Newton, 1994). 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, 1994). 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 nest sites.

This leads to the more general issue related to using 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 accessing cavities situated in high places or with narrow entrances. For these reasons nest-box studies are performed by the vast majority of researchers and have consequently become a standard where the bulk of hole-nesting passerine biology data is collected from. This is also the case for studies of urbanization effects on vertebrates conducted on birds. Birds are an excellent model for this purpose, because many species readily adapt to urban environments, at the same time do not strictly depend on this type of habitat and can also be encountered in non-urbanized areas. Yet, nest-boxes are not the breeding sites in which these birds originally evolved and optimised their breeding performance to. Thus, two major questions arise in the context of the ecology and evolutionary biology of secondary cavity nesters: (i) are urban nest-box populations accurate models for natural populations breeding in the city and (ii) are nest-boxes an ecological trap in cities decreasing the reproductive performance of some species and promoting others?

Only a handful of studies to date 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 (Czeszczewik, 2004; Purcell et al., 1997, but see Norris et al., 2018), larger clutch size (Czeszczewik, 2004; Norris et al., 2018; Robertson & Rendell, 1990), lower predation risks (Mitrus, 2003; Nilsson, 1984; Purcell et al., 1997, but see Czeszczewik, 2004), fledging more young (Norris et al., 2018; Purcell et al., 1997) and having higher nesting success (Llambías & Fernández, 2009, but see Johnson & Kermott, 1994). These patterns appear to vary across species (Mitrus, 2003; Purcell et al., 1997; Robertson & Rendell, 1990). Nest-box studies have been criticised for creating artificial densities of breeding pairs (Alatalo et al., 1991; Camprodon et al., 2008; Cockle et al., 2010; Hagvar et al., 1990; Lõhmus & Remm, 2005), altered nest properties, such as microclimate (Maziarz et al., 2017, Sudyka et al., in prep), ectoparasite loads (Wesołowski & Stańska, 2001) or predation pressures (Czeszczewik, 2004; Mitrus, 2003). All these cues potentially change reproductive strategies: increased breeding density may lead to increased intra- and inter-specific competition, increased extra-pair paternity rates (Mayer & Pasinelli, 2013) or negative density-dependence of reproductive output (Pöysä & Pöysä, 2002) and nest microclimate can alter parasite loads - due to material accumulation in uncleaned nest-boxes (Wesołowski, 2000) - or possibly affect the avian gut microbiome (Maraci et al., 2021). Moreover, higher temperatures in nest-boxes may be relevant for reproduction onset because temperature is a cue for egg laying (Dhondt & Eyckerman, 1979) and likely create a confounding factor while studying heat-island effects in cities. Additionally, even within nest-box studies, it is hard to generalise many conclusions because of major differences in nest-boxes design among studies and its inadequate reporting (Lambrechts et al., 2010). As a result, a number of 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; Czeszczewik, 2004; Mitrus, 2003; Møller, 1989; Purcell et al., 1997; Robertson & Rendell, 1990; Wesołowski, 2011; Wesołowski & Stańska, 2001). 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 & Rendell, 1990; Wesołowski, 2011). Unfortunately, this recommendation is not given much consideration, and since the number of nest-box studies recently emerging in the field of urban evolutionary ecology increases rapidly (Szulkin et al., 2020), knowledge on whether nest type (natural vs artificial) creates a bias regarding our inference of trait distribution may become of growing importance in the near future. This context brings about a major caveat of all up-to-date studies comparing natural and artificial breeding cavities: nest-boxes are generally set-up in secondary forests (Alatalo et al., 1988; Johnson & Kermott, 1994; Llambías & Fernández, 2009; Nilsson, 1984; Norris et al., 2018; Purcell et al., 1997; Rendell & Robertson, 1989; Robertson & Rendell, 1990) apart from two studies in a primeval forest (Czeszczewik, 2004; Mitrus, 2003). This severely limits their relevance to extrapolate results into the 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 nest type effects in two small passerines: blue tits (*Cyanistes caeruleus*, hereafter BT) and great tits (*Parus major*, hereafter GT). These species are the only Western Palearctic Parids doing equally well in terms of population numbers in urban and forest habitats (Bańbura & Bańbura, 2012), and have thus been instrumental in formulating hypotheses addressing the impact of urbanisation on the biology of birds. Specifically, we addressed two questions: (i) is the ecology of nest-boxes different from natural-cavities, leading to varying effects on reproductive outcome, and (ii) do urban birds from natural-cavities and nest-boxes differ in life-history traits (in particular breeding performance)? Because of expected differences in nest properties which can influence clutch size or fledging success, e.g. nest dimensions (Møller et al., 2014), height above the ground (Alatalo et al., 1991; Maziarz et al., 2016) or unstable thermal conditions in nest-boxes while compared to natural-cavities (Maziarz et al., 2017, Sudyka et al., in prep), we predict that nest-boxes will be less productive in terms of clutch size (in GT which should have smaller nests in nest-boxes) and fledging success, even if providing a safer breeding environment (expected less predation than in natural-cavities). Due to varying temperature profiles between natural-cavities and nest-boxes, we also 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.

2. Methods

While we focus here on key methodological aspects of the study, we provide extensive information on natural-cavity vs nest-box ecology in Supplementary Information (SI), such as data on nest dimensions in both natural-cavities and nest-boxes. In SI we also show details on: study species, study sites, nest search and monitoring, second clutches (data inclusion criteria), pilot season, natural-cavities within the nest-box site, variables for main analyses, environmental data collection and weather conditions.

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) where two sites were monitored (Fig. 1) – one with only natural-cavities (BIE, 30 ha core area) and one with nest-boxes (BIB, 15 ha with 65 nest-boxes woodcrete Schwegler 1b, Table S1). We performed intensive nest searches at the natural-cavity site and weekly nest-box rounds on the other study site to record lay date, clutch size, incubation start [actual incubation determined by egg candling allowing to precisely recognize start of embryo development, a technique widely used in poultry industry adopted for small hole-nesting passerines (Ojanen & 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, we recorded the stage of loss or if possible the specific reason (desertions without specific reasons include the following stages: at building, at egg laying/incubation, after hatching; failures with identified reasons: predations on eggs/chicks/of adults and collapsing – i.e. backfilling with dry/decomposed wood material dropping from the cavity – or flooding with rainwater). To characterize the environmental conditions during the reproductive seasons, we collected data on microclimate within nests, food availability (frass fall collection, recorded as grams/m^2/day) at the study sites, weather and noise and air pollution (study area is located within a capital city, thus we also evaluated if noise and air pollution were uniform across the two sites and did not interfere in our study design).

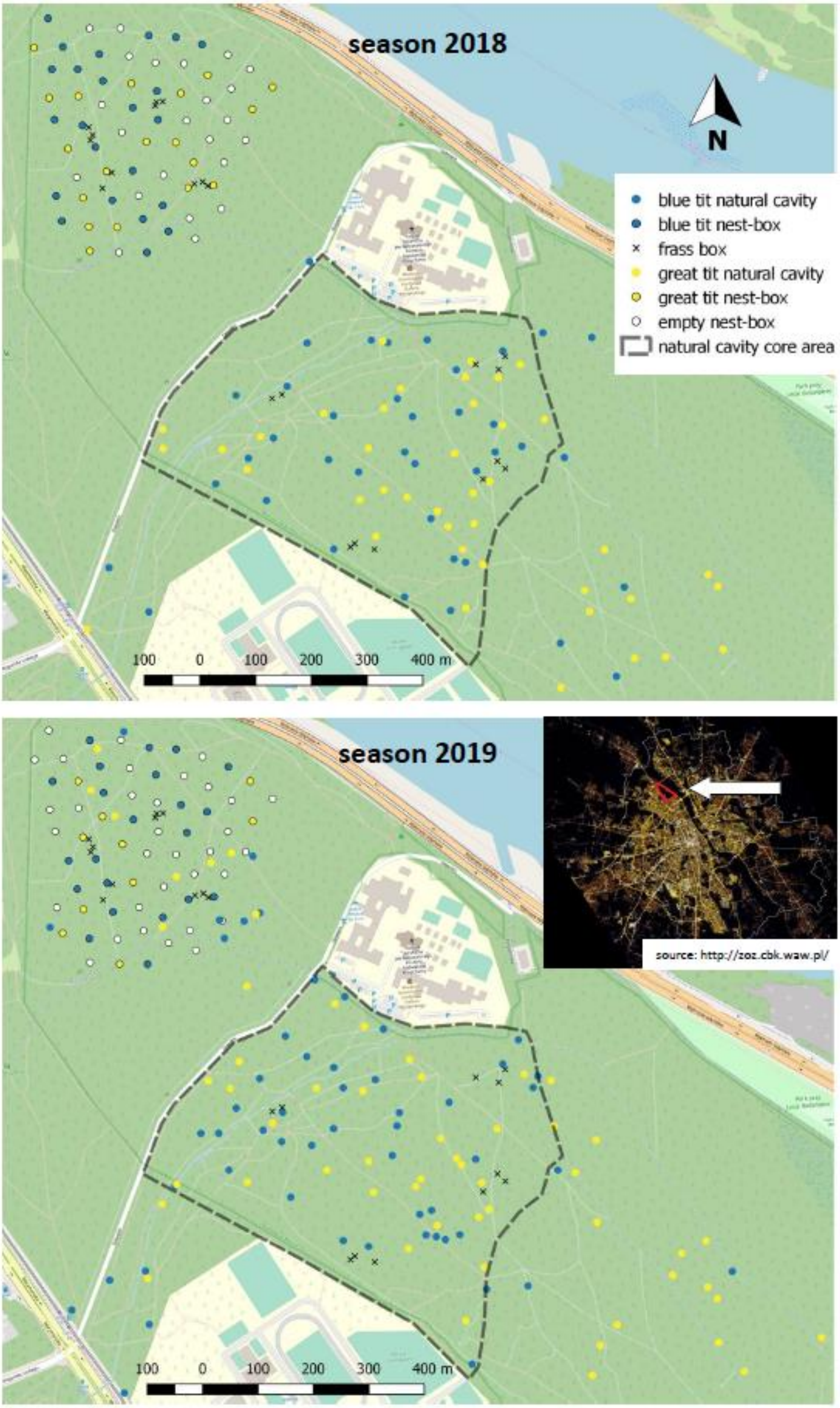

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Fig. 1 Map of the study sites with nest distribution in Bielany Forest in 2018 (top) and 2019 (bottom). The night-time photograph indicates the location of Bielany Forest in the Warsaw city matrix.

Statistical Analysis

Details of statistical analyses of environmental variables and breeding densities, nest-box occupancy and failure rates are presented in SI. To test for potential differences in life-history and fitness parameters between breeding events occurring in natural-cavities and in nest-boxes (SI: '*Variables for main analyses*' for the detailed description of all parameters), we used GLMs introducing nest type (understood as nesting site type: natural-cavity vs nest-box), year and their interaction as explanatory variables. When non-significant, the interaction was removed. We accounted for lay date (fitted as linear and quadratic term) in all analyses (introducing it as a continuous covariate), but retained as either linear or quadratic effect only if significant (and improving model fit using AIC- χ^2 comparing models) as a main term or in interaction. We checked all models for overdispersion and multicollinearity (first, we checked correlation of all studied variables and supplemented this analysis with calculating VIF 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 concerns 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 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 S1). All analyses were performed in R (v.4.0.4) (R Core Team, 2021).

3. Results

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

The natural-cavity site and the nest-box site were highly homogenous in terms of measured environmental variables (Models S1-S3). At the same time, temporal variation was recorded for these variables independently of site location. Food availability was uniform between the natural-cavity and nest-box sites (χ^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 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, Model S1, Fig. S1). Weather patterns were significantly different between years, with 2019 being unfavourable in terms of temperature, humidity and precipitation (SI: '*Weather*', Model S2, Fig. S2). Consequently, 'year' was always kept as a fixed factor in our analyses. Noise levels (mid-range and impulsive) were uniform between sites (χ^2 = 1.565, P = 0.211 and χ^2 = 0.175, P = 0.675 respectively, Model S3A-B) and so was air pollution (both average and maximum concentration of PM 2.5, χ^2 = 0.012, P = 0.912 and χ^2 = 1.318, P = 0.251 respectively, Models S3C-D).

Breeding densities in natural-cavity and nest-box sites are high

The number of breeding BT and GT observed in the natural-cavity site and in the nest-box site was of the same order of magnitude: in 2018, we observed 10.3 pairs of BT and 10.0 pairs of GT/10 ha at the natural-cavity site and 15.3 pairs of BT and 12.7 pairs of GT/10 ha at the nest-box site. In that year, we did not record nesting attempts in cavities in the proximity of nest-boxes, but we did not perform systematic searches. In 2019 we performed such searches and at the nest-box site 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. At the natural-cavity site we recorded 13.3 pairs of BT and 10.0 pairs of GT/10 ha. The overall proportions of BT vs GT nests (without natural-cavities at the nest-box site 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 (χ^2 = 2.847, df = 1, P = 0.092). The proportion of species in both nest types did not differ between years (χ^2 = 0.542, df = 1, P = 0.462).

In 2019, there were fewer nest-boxes occupied than in 2018 (56.9 vs 75.4 % nest-box occupancy by tits) and the occupancy was not affected by nest-box exposition (Model S4). The proportion of species in occupied nest-boxes did not differ between years (χ^2 = 1.491, df = 1, P = 0.222), with more BT than GT each year (Table S2).

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

We were able to determine nesting outcome (success, that is if at least one chick fledged, or failure) in 202 nests in the two study years (97 BT, 94 GT and 11 tit nests that failed before the species could be assigned). Additionally, we identified 59 nests -23 GT and 38 BT- in natural-cavities but these were inaccessible, thus we did not record their outcome. There were no differences in overall failure rate between the nest types [36 out of initially occupied 116 natural-cavities (31.0%) vs 27 out of initially occupied 86 nest-boxes (31.4%, χ^2 = 0.537, P = 0.464, Model S5)], however in 2019 there were more failures than in 2018 [40 out of 101 (39.6%) vs 23 out of 101 (22.8%) nesting attempts). Nest exposition did not influence failure rate (Model S5). The analysis of reasons/stages at which the losses occurred showed differences between nest types (χ^2 = 12.014, P = 0.017, Model S6): in natural-cavities, we observed a higher occurrence of whole clutches predation (7.8% vs 2.3% of all nests) and instances of collapsing and soaking (3.5% vs 0%), while in nest-boxes desertions after hatching (without specific reasons) were more frequent (5.8% vs 1.7%). In both types of nests, the greatest number of nest failures 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 for losses were not significant across years, but they varied between nest types in the two study seasons (significant nest type*year interaction, Model S6 and Fig. 2).

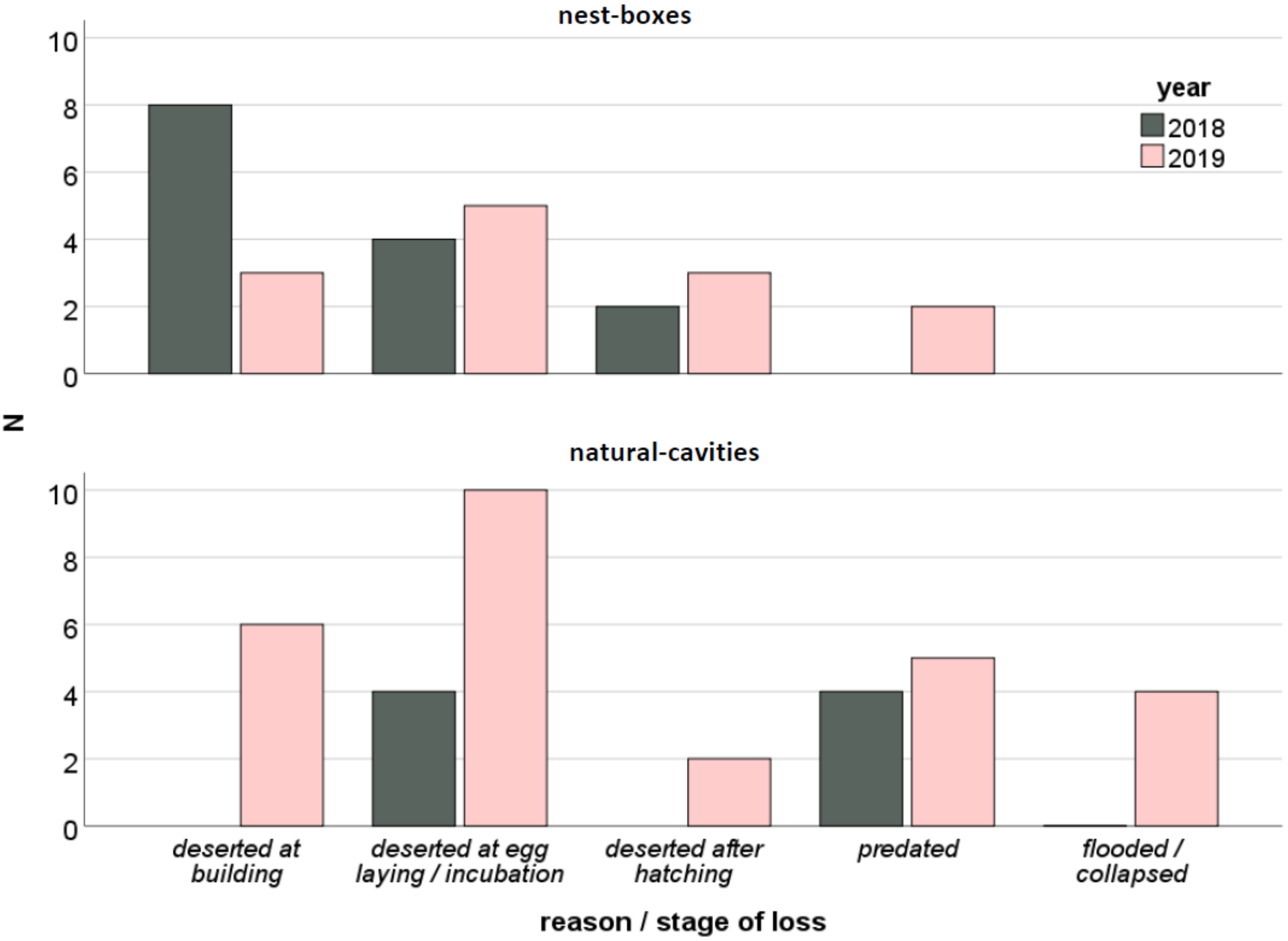


Fig. 2 Reasons/stages for nest losses in nest-boxes (top) and natural-cavities (bottom). Data from 86 nest-boxes (2018: 49, 2019: 37) and 115 natural-cavities (2018: 51, one case where female incubated an empty nest excluded, 2019: 64). Bars show number of cases.

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

All estimates are presented in Table 1.

In both species, lay dates did not differ between natural-cavities and nest-boxes (Fig. 3A-B), but were earlier in 2019 in BT. Importantly, both BT and GT in nest-boxes accelerated the start of incubation in comparison to natural-cavities (Fig. 3C-D). In BT, there was a negative quadratic effect of lay date on incubation start: early and late clutches delayed incubation (Table S3). In GT, incubation start was also delayed in the unfavourable year of 2019 relative to the favourable year 2018. Interestingly, the GT accelerated incubation with later laying dates only in nest-boxes, but lay date did not affect incubation start in natural-cavities (significant interaction lay date*nest type, Table S3).

For both BT and GT, hatching date was not affected by nest type, but BT fledged later in nest-boxes than in natural-cavities (Fig. 4A) and later in 2019. No such relations were observed in GT, and fledging date was uniform between nest types (Fig. 4B) and between years.

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

In BT there was a tendency for higher clutch size in nest-boxes, but the effect was only significant in an interaction with year: in the favourable 2018 there were more eggs in nest-boxes than in natural-cavities but no differences were noted in the adverse 2019. GT laid fewer eggs in 2019, but there were no differences between nest types.

Hatch rate (the ratio of nests with successfully hatched eggs to all nests with at least 1 egg laid) in BT did not differ between nest types, but tended to be lower in the year with poorer weather (2019). Interestingly, BT hatch rate decreased later in the season (with increasing lay date) only in natural-cavities, but not in nest-boxes (interaction lay date*nest type, Table S3). In GT, hatch rate was uniform between years and nest types, but just like in BT, it decreased later in the season in natural-cavities, and increased in nest-boxes (Table S3).

BT hatching success (the proportion of eggs that hatched within a clutch, calculated only for nests that successfully hatched at least one chick) was lower in nest-boxes than in natural-cavities. It was also higher in the adverse year 2019 than in the favourable year 2018. This effect stems from the significant interaction nest type*year: in natural-cavities, hatching success was similar in both years while only in nest-boxes it was lower in 2018 (CS in that year was higher in nest-boxes than in natural-cavities: BT laid more eggs but many failed to hatch). In GT, hatching success was stable across nest 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. As hatch rate and hatching success inform about reproductive output an different nesting stages, our data shows that BT in natural-cavities perform better only after certain stage in reproductive investment is reached (i.e. after hatching). Conversely, before that stage nest type does not influence BT breeding performance.

BT produced less fledglings while nesting in nest-boxes than in natural-cavities (Fig. 5A). Interestingly, for GT, the opposite trend was observed, as GT tended to raise more fledglings in nest-boxes, although the relation was not significant (Fig. 5B). 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. In GT, neither type of nest 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), while in GT there was only a tendency for longer nesting time in nest-boxes (Fig. 4D). 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 (Table S3). Nesting time was uniform between years in both species.

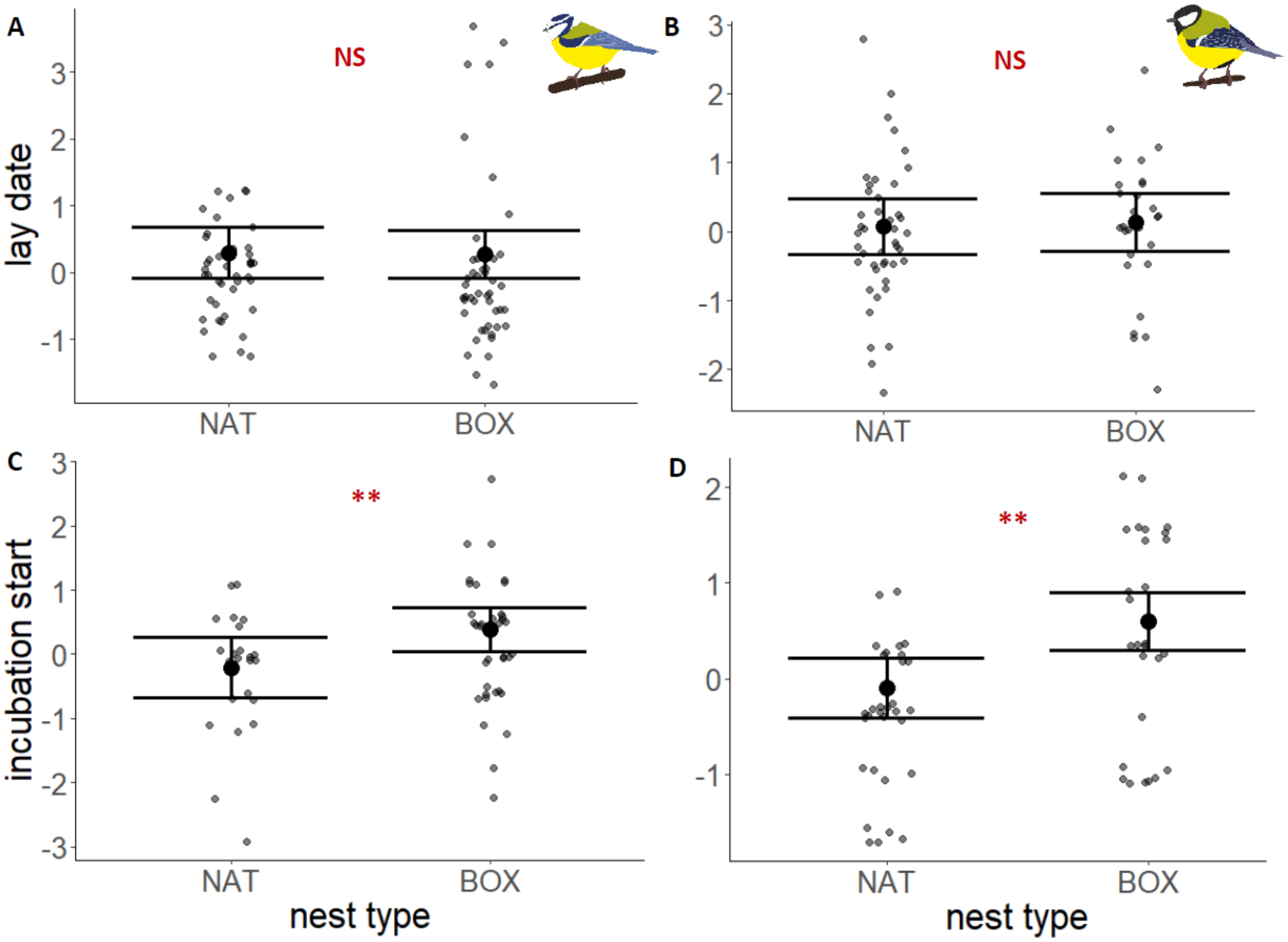


Fig. 3 Lay date (A-B) and incubation start (C-D) of blue tits (A, C) and great tits (B, D) breeding in natural-cavities (NAT) and nest-boxes (BOX) in Bielany Forest. Predicted values ± 95% CI are shown on Z-score scaled response variables in days. Significance levels for nest type: NS: not significant, **: 0.001<P<0.01.

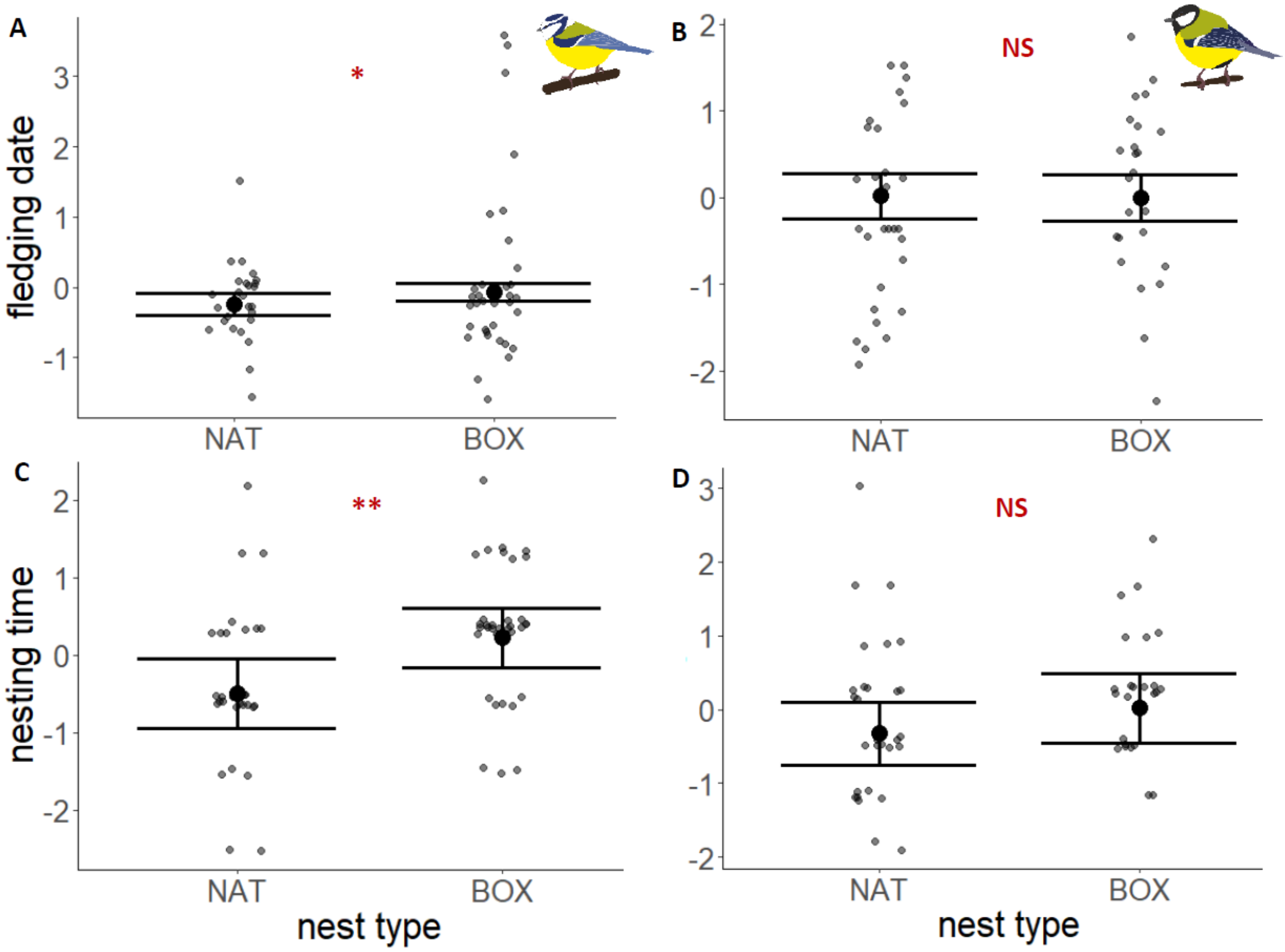


Fig. 4 Fledging date (A-B) and nesting time (the number of days from hatching till fledging; C-D) of blue tits (A, C) and great tits (B, D) breeding in natural-cavities (NAT) and nest-boxes (BOX) in Bielany Forest. Predicted values ± 95% CI are shown on Z-score scaled response variables in days. Significance levels for nest type: NS: not significant, *: 0.01<P<0.05, **: 0.001<P<0.01.

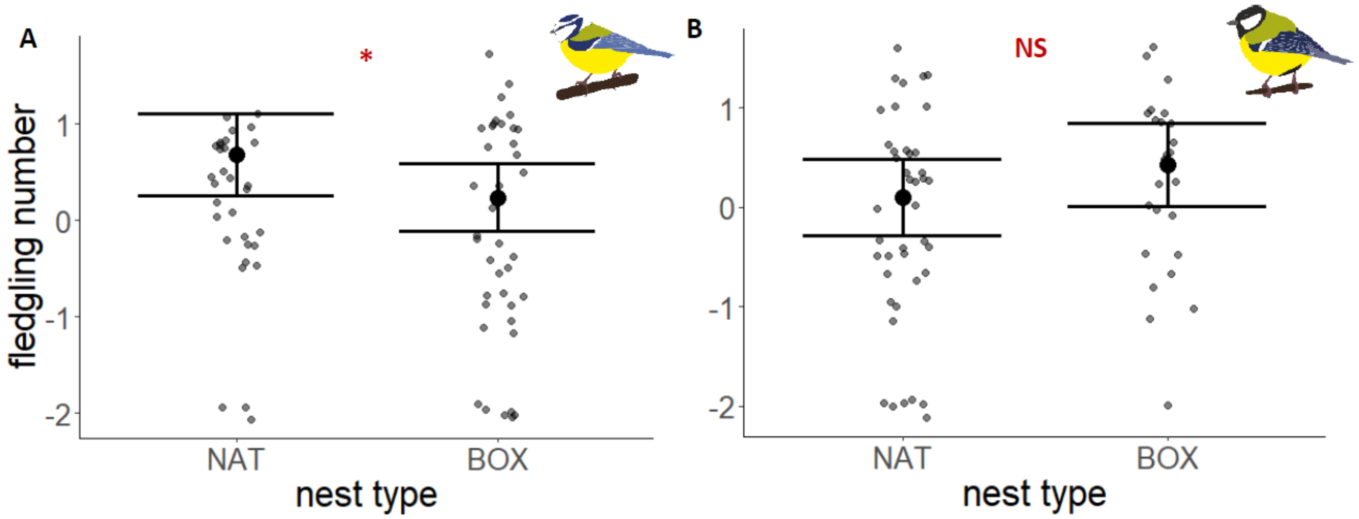
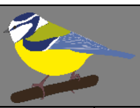


Fig. 5 Number of fledged young of blue tits (A) and great tits (B) breeding in natural-cavities (NAT) and nest-boxes (BOX) in Bielany Forest. Predicted values ± 95% CI are shown on a Z-score scaled response variable. Significance levels for nest type: NS: not significant, *: 0.01<P<0.05.

Table 1. 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. We retain and present the interaction of the two main factors only if significant. Natural-cavity and 2018 are the references for the estimates and all estimates are shown after Z-score scaling of continuous variables. In all models we additionally accounted for lay date and present the estimates in Table S3, but these were retained only if significant (as a main factor or in interaction). Sample sizes for each analysis are shown in Table S4. Estimates for significant (P<0.05) factors are indicated in bold, trends (P<0.20) in italics.

Nest Data	**Blue tits** 						**Great tits** 					
	Nest type		Year		Nest type*Year		Nest type		Year		Nest type*Year	
	Estimate ± SE	Pr(> χ^2)	Estimate ± SE	Pr(> χ^2)	Estimate ± SE	Pr(> χ^2)	Estimate ± SE	Pr(> χ^2)	Estimate ± SE	Pr(> χ^2)	Estimate ± SE	Pr(> χ^2)
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**	**0.0004**	**-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**	**0.0002**		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**	**0.00004**		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

Nest dimensions: no correlation with phenology or fitness proxies

For nesting, tits used natural-cavities formed mostly in hornbeams (*Carpinus betulus*) and oaks (*Quercus robur*, Fig. 6). Natural-cavities of both species were situated higher above ground level than nest-boxes (Table S1 for all nest dimensions and test results). Importantly however, in GT, accessible cavities with known nesting outcome were no different in respect of height from nest-boxes. 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 always lower in nest-boxes. In both species, nests in natural-cavities were much deeper and safety distance – the shortest distance from 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.

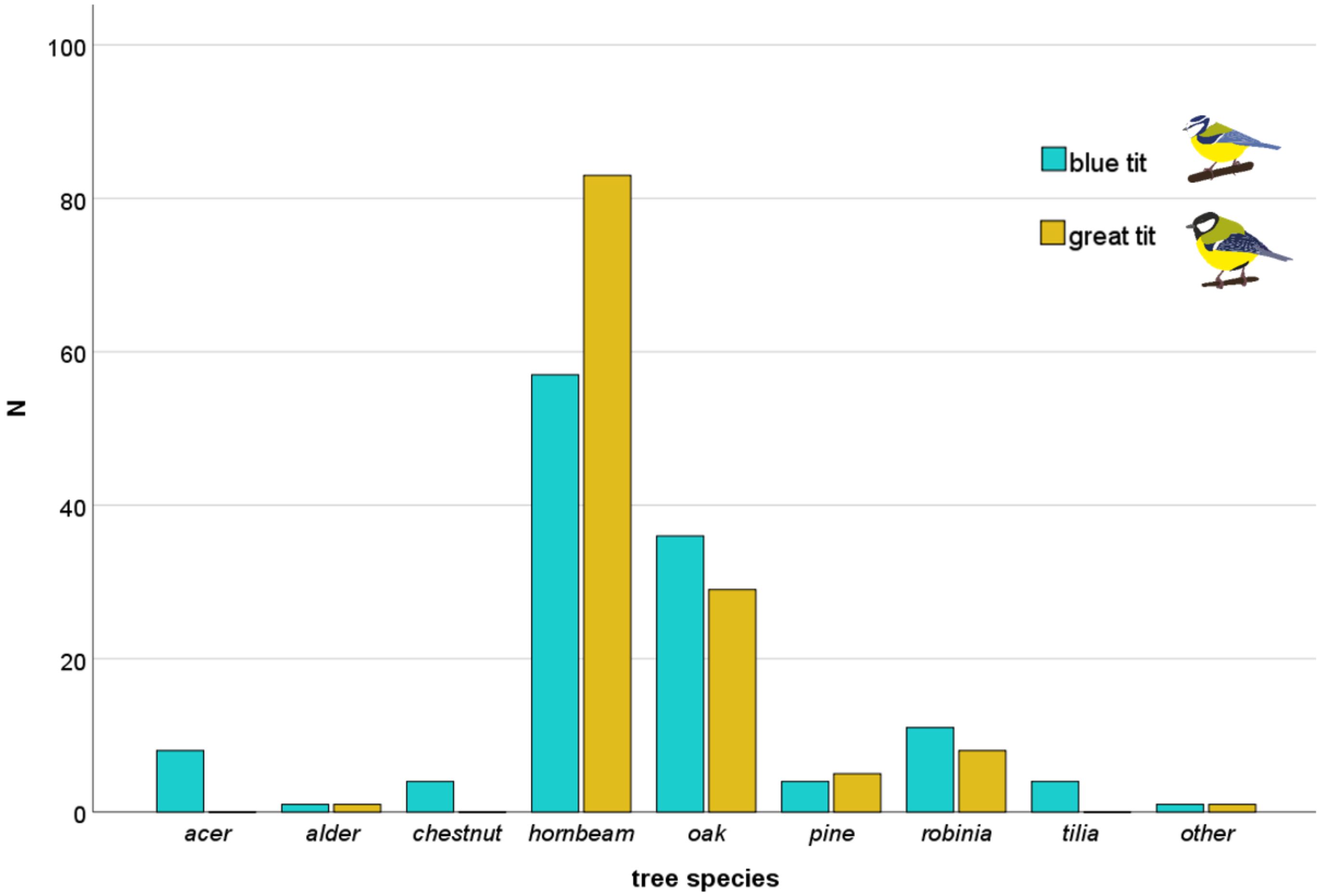


Fig. 6 Tree genera used by tits for nesting in natural-cavities in the three study seasons (2017-2019) in Bielany Forest. Bars show number of cases.

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 1) and in the model on nesting failures (Model S6), but these invariably and in both species did not impact (all P>0.05) lay date, clutch size, number of fledglings, fledging success, nesting time and nesting failures. As such, they were removed from the final models.

4. Discussion

This is the first study to compare fitness consequences of breeding in artificial nesting sites as opposed to natural-cavities in an urban setting. More generally, this is also one of the very few studies explicitly testing differences in passerine life-history traits and fitness variation when inferred from natural-cavities and nest-boxes in a quasi-experimental setting. We demonstrate that the type of nesting site 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). Chicks also spent more time in the nest (Fig. 4C, nesting time: from hatching till fledging), and fledged later in the season (Fig. 4A) than the natural-cavity-nesting birds. In GT, differences in breeding parameters between natural-cavities and nest-boxes were not apparent (Figs 3-4), and their breeding performance was similar or even tended to be better in nest-boxes than in natural-cavities (e.g. the tendency for higher fledgling number, Fig. 5B). Importantly, both species experienced shifts in the onset of natural incubation as they were found to start incubating earlier in nest-boxes (Fig. 3C-D), which can lead to increased hatching asynchrony (Stenning, 1996).

Reproductive outputs

Our results indicate that urban BT are more sensitive to the artificial nesting sites than GT. The deterioration in fledging success and fledging number (Fig. 5A), parameters that are directly related to fitness, shows that nest-boxes may not be optimal breeding places for this species, but are completely sufficient for GT. This may be in line with observations of larger breeding density of GT than BT pairs in some urban settings [>3 times in southern Finland, with no major differences between rural populations of both species (Solonen, 2001)]. In Warsaw, in the two study years we observed marginally larger GT than BT breeding densities across six urban sites (mean ± SD/10 ha: 7.6 ± 3.7 vs 6.7 ± 4.7), but also more GT than BT were breeding at a rural site (5.0 vs 1.9). Despite these local differences, the urban populations of both species appear to be stable in numbers (Bańbura & Bańbura, 2012). This is usually explained by high overwinter survival on human-provided food (Chamberlain et al., 2009), but our results indicate that the type of nesting site usually provided in cities may also influence the numbers of these urban birds. Nevertheless, GT fledgling numbers remained unaffected by the type of cavity (natural or artificial) they were reared in. These results complement earlier studies comparing the reproductive output stemming from natural-cavities and nest-boxes. Thus, 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 & Fernández, 2009; but see Czeszczewik, 2004; Robertson & Rendell, 1990). 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 & Rowiński, 2012). Likewise, our study did not confirm this relationship and the differences in nest sizes between nest types were noted only for GT and not BT (Table S1). Since in our study there were no overall differences in clutch size and hatching rates between nest types (i.e. pre-hatching investment, Table 1), the observed effects on fledgling numbers 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 nest properties or investment of parents. We were not able to detect the influence of nest dimensions (Table S1) on various fitness outcomes and we did not measure parental investment (provisioning rates) between the two types of nests, thus we are not able to exclude such differential investment according to nest type. However, our data on microclimate (Sudyka et al., in prep) indicate that nest properties may underlie the observed differences. Worse reproductive outcomes may also be noted in species which are poor competitors for (Norris et al., 2018) - or have a preference towards - a particular nest type. In accordance with this prediction, some studies suggested natural-cavity preference in BT and nest-box preference in GT, although on small sample sizes (Lõhmus & Remm, 2005). Our data does not allow to formally test about the preference of nest-boxes over 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 both species: BT and GT bred in both types of nests if available at the same plot (SI: ‘*Natural-cavities within the nest-box site*’, Table S5).

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 determined by the rates of mortality inside the nest as opposed to outside of it (Martin et al., 2018). In our study setup, outside mortality rates are independent of nest type, because after fledging all birds share the same environment, but what differs is the pressure experienced inside the nest: predation was lower in nest-boxes in our study (Fig. 2, Model S6), similarly to other comparative works (Mitrus, 2003; Nilsson, 1984; Purcell et al., 1997). Thus, staying longer can be optimal in safer nest-box environment. Alternatively, greater temperature amplitudes experienced by the young in nest-boxes (Sudyka et al., in prep.) 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 hamper BT fitness: birds which fledge later have worse lifetime reproductive success after recruitment (Visser & Verboven, 1999), lower probability of survival (Cooke et al., 1984; Naef-Daenzer et al., 2001; Perrins, 1965) and produce less recruits into the breeding population (Naef-Daenzer et al., 2001, but see Monrós et al., 2002). This may additionally impact the numbers of urban BT because the availability of natural-cavities in most urban habitats is decreased in comparison to rural ones

(LaMontagne et al., 2015) and urban BT and GT may have a reduced tendency to migrate and disperse (Bańbura & Bańbura, 2012).

For the first time, we show that nest 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 youngest chicks (Stenning, 1996). Interestingly, GT accelerated incubation with later laying dates only in nest-boxes, but lay date did not affect incubation behaviour in natural-cavities, possibly due to the fact that temperature and humidity are stable throughout the breeding season in natural-cavities (Sudyka et al., in prep). Such phenological shift is yet another factor that could influence reproductive outcomes of tits breeding in nest-boxes.

Contrary to some previous studies (Czeszczewik, 2004; Purcell et al., 1997), we did not detect earlier lay dates in nest-boxes (but see Norris et al., 2018). This lack of effect may stem from the fact that in early spring, nest-boxes are on average warmer than ambient temperature [high temperature is a cue for advanced lay date (Dhondt & Eyckerman, 1979)] while natural-cavities are cooler, but due to better insulating properties in cavities, nest-boxes become colder at night than natural-cavities (Sudyka et al., in prep).

Breeding densities and nesting failures

Providing nest-boxes generated tit breeding densities of the same order of magnitude relative to that observed at the natural-cavity site. More specifically however, it appeared to increase tit local densities in an urban habitat with available natural-cavities, though this could not be formally tested due to limited sample size. Nevertheless, abundant natural-cavities provide opportunities to nest only a couple of meters apart (we recorded several such cases over the three study seasons) or even in the same tree at the same time (in 2019 a BT pair occupied a higher cavity and a GT a lower one, and both broods successfully fledged). In contrast, nest-boxes are usually distributed in arbitrary intervals, which may hamper optimal usage of the best habitat patches, normally capable to support more than one breeding pair. Importantly, breeding densities were very high in both the natural-cavity plot, and even more so in the nest-box plot (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; unpublished data). The average density in oak-hornbeam-lime forest patch in Białowieża National Park (BNP, treated as a baseline primeval ecosystem for breeding densities) is 4.0 pairs/10 ha for BT and 4.9 pairs/10ha for GT (Wesołowski et al., 2010). Thus, the breeding densities recorded in the natural-cavities of a primeval forest are almost three and two times lower than what was recorded at our urban natural-cavity site for BT and GT (respectively), and almost 4.5 and 2.5 times lower than what was recorded at our nest-box site for BT and GT (respectively). Importantly, 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 strongly suggests that tit breeding densities are not necessarily driven by the availability of natural-cavities (which are in surplus in both the primeval forest and in our urban site). Rather, they are likely to be the result of other ecosystem attributes and dynamics, which undoubtedly deserve further work.

We did not detect differences in overall nesting failure rates between the two types of nests. In natural-cavities, height above ground may be important for nesting failures (Alatalo et al., 1991; Rendell & Robertson, 1989), but it was not correlated to the failures in our study. In primeval habitats (such as BNP) 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. However, we confirmed that reasons for failures differed between the types of nests (Model S6, Fig. 2). 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 paucity of natural predators in Bielany Forest and close human presence [especially when compared to BNP predation rates (Maziarz et al., 2016; Wesołowski & Rowiński, 2012)], but lower in nest-boxes in accordance with previous work (Llambías & Fernández, 2009; Mitrus, 2003; Møller, 1989; Nilsson, 1984; Purcell et al., 1997). Yet, predation rate appears to be year-dependent, since in the pilot season 2017 at the natural-cavity site it was three times higher than in the remaining two seasons, exceeding 21%, SI). Nest-boxes appear to be safer despite the fact that nest depth and safety distance are greater in cavities (Table S1; if chicks are already grown and are able to move towards the entrance they can become easy prey for predators such as woodpecker despite the large nest depth). Predators can have difficult access, because opening holes in nest-boxes have smaller vertical dimension and are narrower (in case of GT), which may suffice as protection in the type of habitat with relatively low predation pressure. Yet, the 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 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.

Year-specific effects

The effects of nest-box provisioning can be difficult to detect over the short term (Valera et al., 2019). The comparative part of our study took place for only two breeding season, thus we cannot generalize these results as reflecting long-term, population-level consequences resulting from nest-box use. However, the breeding seasons in which we conducted our study give an opportunity to compare nesting outcomes in the two types of nests in a favourable and an unfavourable season. 2019 was an unpredictable year with a warm pre-breeding month (March) and cold and humid months crucial for reproduction (April, May, Model S2, Fig. S2). Weather conditions are essential for caterpillar availability (Wesołowski & Rowiński, 2014), and indeed, in May 2019 there was on average more than three times less caterpillars than in May 2018 (mean ± SD: 0.27 ± 0.04 vs 0.90 ± 0.20, Model S1, Fig. S1). Unfavourable weather can additionally obstruct effective foraging for caterpillars by tits. The year effect was visible in many traits under study: in 2019 fewer nest-boxes were occupied, nesting failure rate was higher, both species delayed incubation, BT started laying earlier and GT clutches were smaller and most importantly, independently of nest type, fledgling number was lower in both species (and fledging success also in BT, Table 1). Many trade-offs can only be visible if resources are scarce or when the environment is harsh (Stearns, 1992), thus we can treat (with caution) our diverse study seasons as a naturally occurring experiment. In this light, for some parameters, the effect of nest type was detected only in the adverse 2019 year: we recorded lower clutch size in nest-boxes while compared to natural-cavities in BT (however hatching success of BT in nest-boxes was lower from natural-cavities only in 2018) and hatching success in GT (Table 1).

Study limitations

It is unlikely that the observed differences between natural-cavities and nest-boxes stem from varying quality between parents using the two types of nests. First, because birds using both types of nests come from the same population and at each of the plots (BIE or BIB) they did not need compete for the two types of nests on the same area as these were spatially distinct (Fig. 1). In Bielany Forest, the nest-boxes were newly introduced at the beginning of 2018, there was thus no possibility to establish specific phenotypes related to the nesting place type in such short time (for example via preference to breed in the same type of nest 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 vs nest-boxes (Di Lecce et al., in prep; Janas et al., in prep).

While this study focused on comparisons between natural-cavities and woodcrete nest-boxes, one can argue that birds in wooden nest-boxes may exhibit breeding parameters more similar to those observed in natural-cavities. Nonetheless, microclimatic conditions in wooden boxes do not differ substantially in terms of temperature and humidity from woodcrete ones, as both types of nest-boxes provide poor insulating properties while compared to natural-cavities (Sudyka et al., in prep). Next, the bottom area and internal space for nest construction (i.e. nest depth and safety distance) in woodcrete nest-boxes are also similar to wooden nest-boxes (Sudyka et al., in prep). Moreover, other studies directly compared natural-cavities and wooden nest-boxes and detected differences in various breeding parameters (Norris et al., 2018; Purcell et al., 1997).

An outlook on the ecological importance of old-growth tree stands in cities

The results of our study indicate that nest-boxes may turn out to be an ecological trap for some species (thus, for BT, but not for GT, nest-boxes were a poorer habitat than natural-cavities), while other species can benefit greatly and win inter-specific competition for the same pool of nesting sites in the long run. Within the urban space, places such as cemeteries and large urban parks, especially with present snags (standing, dead or dying trees; Blewett & Marzluff, 2005), are able to upkeep biodiversity of nest excavators such as woodpeckers (Bovyn et al., 2019; Smith & 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 availability, that determines secondary hole-nesting bird abundance in managed forests; thus, in 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, the existence of large old-growth stands, such as Bielany Forest, within urbanised areas is of great importance for cavity-nesting urban birds (and other non-avian taxa using them). At the same time, nest-boxes can be a useful source of nesting sites in areas where no natural-cavities are available, including urban areas. Given that cities and countries lead different policies regarding the maintenance of older trees that can act as providers of natural-cavities, a valuable perspective could stem from modelling work identifying times when nest-boxes ought to be provided, and conditions under which natural-cavities may suffice – this study is the first to our knowledge to provide quantitative estimates of breeding success in urban natural-cavities and nest-boxes under standardised environmental conditions. These could be used as entry parameters for further modelling work on the benefits stemming from natural-cavities and nest-boxes in the urban space.

5. Conclusion

Our study has several meaningful implications to understand how nest-boxes can impact the breeding performance of urban birds. First, we note that the effects of nesting site type are not uniform across species: in BT, the most important fitness proxies that could be inferred in both nest types (e.g. fledging success, fledgling numbers, time spent in the nest and fledging date) were sensitive to nest type and resulted in lower values in nest-boxes, while GT performance appeared not to be affected by nest type (with the exception of shifts in incubation patterns, which ultimately did not result in differential fitness outcomes).

In this light, do we have convincing evidence that studying urban birds in nest-boxes can answer our general questions on bird physiology/life-history responses to the urban environment given all potential confounding effects related to this artificial nesting site? 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 & Rendell, 1990; Wesołowski, 2011), particularly in areas where the availability of natural-cavities is likely to outnumber the contribution of nest-boxes at the population level. Moreover, in urban habitats, other artificial nesting sites – such as mailboxes, lamp posts etc. – may outnumber the availability of both natural-cavities and nest-boxes. Thus, nest-box provisioning programs may only be beneficial if nest-box reproductive outputs are better than that in the other artificial nesting sites, especially because density dependence may further limit reproductive outputs and negate management actions (Pöysä & Pöysä, 2002). We thus encourage study of all types of nesting sites available in cities to discover pivotal factors in determining urban cavity-nesters population dynamics.

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Ethics

All applicable institutional and national guidelines for the care and use of animals were followed. Permit numbers to work with birds on the natural-cavity site: WPN-I.6401.80.2017.ŁM and WPN-I.6205.53.2017.AS and on the nest-box site: WPN-I.6401.515.2017.KZ and WPN-I.6205.227.2017.AS issued by RDOŚ and LM-W.LO.400.88.2017.DC1460 issued by Lasy Miejskie – Warszawa.

Author contributions

JS developed the concept with contributions from IDL, LW, PR and MS; JS, IDL, LW and PR collected the data in the field; MS assisted in fieldwork; JS analysed the data; JS led the writing of the manuscript. All authors contributed critically to the drafts, agreed to be held accountable for the content therein and approved the final version of the manuscript.

Data Availability Statements

Data are available in the online Supporting Information, and will be made available in an online repository upon publication following peer-review.

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Competing interests

We declare no competing interests.

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Supporting Information

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

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A blue tit provisioning young with a caterpillar in a natural-cavity of Bielany Forest. A light rod is visible at the bottom of the cavity's entrance (photo J. Sudyka)

1. Study species

Blue tits (*Cyanistes caeruleus*, hereafter BT) and great tits (*Parus major*, hereafter GT) are small passerines (~11 g and ~17 g respectively) with maximum longevities of 12 and 15 years respectively recorded in the wild (Euring database). The average age of breeding individuals may vary across populations: for example, the average age of breeding GT females is 1.81 years (Bouwhuis et al., 2009) and the median age for BT is 2 years (Sudyka et al., 2014; Sudyka et al., 2019). Both parents perform parental care, such as chick provisioning and nest sanitation (Bańbura et al., 2001). Females usually lay one clutch per season, incubate for ca. two weeks and the majority of nestlings within a nest hatch synchronically. Nestlings are fed mostly with caterpillars, supplemented by spiders and dipterans (Wesołowski & Rowiński, 2014). They fledge 17-22 days after hatching. Blue tits and great tits are cavity nesting species (Wesołowski, 2000), they naturally breed in tree cavities formed as a result of natural wood decay processes (for that they need old forests with old trees) or excavated by other species such as woodpeckers (however these are avoided by them in primeval forests - ca 2% of nests are situated in woodpecker-excavated cavities), but also readily breed in nest-boxes provided by humans.

2. Study sites: the natural-cavity site (BIE) and the nest-box site (BIB)

As a remnant of the European primeval forest, Bielany Forest (ca. 150 ha) is protected under a natural reserve and the Natura 2000 schemes for its unique ecological attributes. At the same time, Bielany Forest is surrounded by dense urban matrix in the city of Warsaw. Since natural corridors connect it (via Młociny Park and Forest and Vistula river valley) with Kampinos National Park (a large, protected forest of 38 544 ha), wild boars, roe and red deers, foxes and hares are its common fauna. Bielany Forest is home to ca. 40 species of nesting birds and natural nest predators include woodpeckers, martens and squirrels. It is composed of several habitats, mainly consisting of hornbeam (*Carpinus betulus*) - and common oak (*Quercus robur*)-dominated stands alongside fragments of riparian forest and European spruce (*Picea abies*). The study was conducted over three consecutive field seasons (2017-2019) within two sites: natural-cavity (BIE) and nest-box (BIB). The two sites were separated by a local, ca. 4 m - wide road (Dewajtis). Central points of both areas were separated by ca. 750 m and the edges by at least 200 m shortest distance (see Fig. 1).

The natural-cavity study site (BIE) was in the SE part of the reserve (52°17'32.2"N 20°57'34.0"E), and consists of a 30 ha core area (where nest searches were the most intense) and 50 ha monitored of hornbeam-oak stands with >100 years succession. For nesting, tits used mostly cavities formed in hornbeams and oaks (Fig. 6). The nest-box study site (BIB) was located in the NW part of the reserve (52°17'52.1"N 20°57'09.7"E), and comprises 15 ha of oak-hornbeam stands with >100 years succession. In early 2018, we installed 65 nest-boxes (woodcrete Schwegler 1b, with no protective devices against predation, see dimensions in Table S1) located 50 meters apart from each other (density: 43 nest-boxes per 10 ha), thus the comparative part of our study comprises two breeding seasons. Nest-boxes had a median height to the entrance of 2.91 m (range: 2.91 to 2.96 m) and were orientated in random exposition (no difference in exposition across 8 cardinal and intercardinal directions $\chi^2 = 8.477$, N = 65, df = 7, p = 0.292).

3. Blue tit and great tit nest search and monitoring

We performed intensive nest searches at the natural-cavity site from the beginning of April to record all breeding attempts of BT and GT. Every day, for 2-3 weeks, three to seven field assistants were searching for birds engaged in nest building. The searches were continued less intensively after we identified most nests and observed reduction of building activity (in May we continued intense searches to localize nests of parents that failed their first clutch). At the same time, we started weekly nest-box rounds on the other study site. On both sites, after identifying an active nest, we started individual nest monitoring. We reduced the number of visits to a minimum. To inspect natural-cavities, we used a portable led light and a mirror for deep cavities or a Teslong NTS200 Digital Endoscope (NovoTech Industries Ltd., 8.2 mm, and a 5 m-long endoscope). Wherever possible, we recorded lay date (LD), clutch size (CS), incubation start [IS, actual incubation determined by egg candling allowing to precisely recognize start of embryo development, a technique widely used in poultry industry (Liu & Ngadi, 2013) adopted for small hole-nesting passerines (Ojanen & Orell, 1978) and used by us in this field study], hatching date (HD), 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, we recorded the stage of loss or if possible the specific reason (desertions without specific reasons include the following stages: at building, at egg laying/incubation, after hatching; failures with identified reasons: predations on eggs/chicks/of adults and collapsing – which means backfilling with dry/decomposed wood material dropping from the cavity – or flooding with rainwater). Chicks underwent all basic biometric measurements at the age of ca. 14 days (hatching day=day 0) and adults were caught while feeding nestlings. They were either captured with mist nets set in the vicinity of the nest ca. 14 days after chick hatching or with traps installed inside nest-boxes, which occurred in most cases ca. 10 days after chick hatching. Nest dimensions in both natural-cavities and nest-boxes (Table S1) were measured using a measuring tape (precision 0.1 cm), and in case of high and inaccessible cavities, nest height was measured with an altimeter/clinometer (Suunto PM-5/1520) that allows to convert the measured angle into absolute height of the object (precision 0.25 m). Depending on cavity height, nests were reached from the ground, with a ladder or using special spikes for climbing. All nests were marked for coordinates (GPSMAP 64s, Garmin). Maps and area counts were made using QGIS open software v. 2.18 (QGIS Development Team, 2020).

At the natural-cavity site, cavities were superabundant (there were always more cavities available than actually occupied), but the same cavities could be reused from year to year. Thus, in 2019 ca. 21% of all active cavities (20 out of a total of 95) had been used in the two preceding seasons. Importantly, in case of natural-cavities, there was no need to clean the nest material (mostly consisting of moss and hair/feathers) as it decomposes naturally over one year due to microclimate and a rich assemblage of decomposing organisms inherent to the cavities. Indeed, Wesołowski (2000) found some remains of previous season nests only in 6% of the cavities that previously contained tit nests. We cleaned nest-boxes twice a year, after the 15th of October to remove nest remains gathered over the breeding season and in January/February to remove winter roosting remains, because some ectoparasites are more numerous in uncleaned nest-boxes

(Rendell & Verbeek, 1996). Thus, the baseline nesting conditions for both types of nests remained alike at the start of each breeding season.

4. Second clutches

Second clutches were defined as a second nesting attempt after successfully fledging young in an earlier nesting attempt. To identify them, we excluded clutches with lay date (LD) later than the earliest fledging date for a given year and species, and this method corresponded the most accurately with our observations of actual second clutches of known (ringed) parents in the field. We did not remove repeated clutches (delayed nesting attempt after a loss). Second clutches were very rare [five clutches out of a total of 282 across 2 years (1.8%)] and were consequently removed from the analyses, both because of them being exceptional and because parental investment in such clutches may differ considerably from the first ones (Lambrechts et al., 2012). In 2018 we observed only one case of second clutch of a GT in natural-cavity. In 2019 we had one second clutch of GT in a natural-cavity and three in nest-boxes (two GT and one BT, see Table S2). In three of these cases we recorded the same parental pair attending their second clutch (2018: 1 GT in a natural-cavity and 2019: one GT and one BT in nest-boxes). In two of these cases (2019: one GT in a nest-box and one GT in a natural-cavity) we did not record first breeding event of the parents, so we may not be sure that these were actual second clutch of these parents but due to a very late LD (after first chicks of the season fledged) these clutches were removed according to our rule of thumb.

5. Pilot season 2017

In 2017, we conducted pilot studies to determine the numbers of tits breeding in natural-cavities of Bielany Forest in order to assess feasibility of our comparative study. In that pilot year, we found 32 BT nests (plus two second clutches) and 24 GT nests (plus five second clutches). Out of the BT nests, 14 nests successfully fledged chicks (including one second clutch), eight nests resulted in nest failure (including one second clutch); no information was available about the remaining ones since they were inaccessible. Out of the GT nests, 13 successfully fledged chicks (including three second clutches), and 10 nests resulted in nest failure (two of them were second clutches). No information was available about the success of the remaining GT broods as they were inaccessible. Overall, 15 first clutches of both species failed to succeed (no chicks fledged) out of 38 first clutches with known outcome (39.5 %). Three (7.9 % of all nests) were deserted at incubation, two (5.3 %) after hatching, eight (21.1 %) were predated and two (5.3 %) collapsed. We monitored all these nests, but the data were not included in this paper as we did not have the nest-box site for direct comparison and we did not collect environmental data on microclimate and food availability in 2017. Thus our comparative study comprises two breeding seasons.

6. Natural-cavities within the nest-box site

In 2019, we identified 17 nests in natural-cavities (16 first clutches, one second clutch) within the nest-box site (with 40 out of 65 nest-boxes occupied by tits) in the course of a systematic search (the same as on natural-cavity site). Within first clutches, we found seven BT nests in which we confirmed only one successful fledging (two nests were inaccessible, so we were not able to confirm their outcome) and nine GT nests (four were successful, and two inaccessible). We captured four parents (two BT and two GT) from two nests and were able to measure 19 chicks from three nests (two GT and one BT).

Because of this limited information, we only present basic statistics in relation to nest-boxes and other cavities in the 2019 season (see Table S5). We removed these nests from the main analyses comparing nest types, because (i) of their low occurrence, (ii) we recorded them systematically in only one of the two seasons, and (iii) different subsets of birds (e.g. of different quality) can occupy natural-cavities and nest-boxes as a result of competition in the same area (summary statistics in Table S5 below). We collected this data mainly to see if/how many birds chose to nest in natural-cavities when artificial nests were provided. Our data does not allow to formally test and draw conclusions on which type of nest (natural or artificial) is preferred by tits when given a choice, since we collected them in one season only (a season with unfavourable weather conditions and lower food availability while compared to the previous one) and the sample sizes are too low (the outcomes would be mainly driven by stochastic effects).

7. Variables for main analyses

All variables used for main analyses are presented in Table 1 of the main text and sample sizes for these analyses are presented in the Table S4 below.

Lay date (LD), most of the LDs were observed directly (i.e. date of laying the first egg, number of days from April 1st), but in 11 % of cases (18/161) it was estimated from incubation stage [determined by egg candling (Liu & Ngadi, 2013; Ojanen & Orell, 1978) – a method allowing to determine the stage of embryo development with the accuracy of ± 1-2 days] or hatching date.

Clutch size (CS), in some nests, eggs were accidentally broken (five nests: three BT and two GT; four nest-boxes and one cavity). If an egg was broken during egg laying we analysed the final observed CS, because the bird could compensate for the broken egg by laying a "replacement" (two nests). If an egg was broken after incubation onset we added the broken egg to the final observed CS for analyses (three nests). For hatching success analysis we counted the broken egg as if it had hatched, since the probability that we broke an egg that would normally hatch was greater than breaking an infertile egg (mean hatching rate per nest for both species: 0.94 ± SD 0.102). In one of the nests two eggs broke at egg laying (a nest-box BT in 2019) and we excluded this nest from analyses on hatching success, number of fledged young and fledging success also because the male abandoned the nest and we cannot be sure if our interference was the cause.

Incubation start (IS), usually tits start incubating after laying their last egg in a clutch, but it can also happen that they accelerate or delay the start of incubation (e.g. due to environmental conditions). In this study, we observed the actual start of incubation via egg candling and compared it with the expected date the incubation should start (which is LD + CS). Thus incubation start was quantified as the difference (in days) between the expected and actual incubation start (negative values denote delayed incubation, while positive accelerated incubation).

Hatch rate (HR), ratio of nests with successfully hatched eggs to all nests which had at least one egg laid.

Further nest parameters were observed and analysed only for nests that successfully hatched (at least one chick hatched).

Hatching success (HS), is the proportion of eggs that hatched within a clutch (hatchling number/CS; hatchling number calculated as CS – number of unhatched eggs: some chicks died between hatching and first check and were removed by the parents, so the number of unhatched eggs provides a better proxy for actual hatchling numbers than counting chicks present around the time of hatching).

Hatching date (HD), most of the HDs were observed directly (i.e. date of hatching of the first egg, number of days from April 1st), but in 16 % of cases (25/155) it was estimated from chick size and/or appearance or predicted from the recorded degree of incubation. This occurred if we missed the actual HD in cavities with difficult access or if a nest was discovered at feeding (accuracy of such estimates is ± 1-2 days, unless chicks are already grown, beyond 10-12 days of age).

Fledgling number (NFL), number of chicks that successfully left the nest. If a chick died during manipulation at day 14 (hatching date = 0; seven chicks in six nests - five BT and one GT - out of total 918 chicks processed in two years, including BIB cavities and second clutches, 881 without these) we used the number of chicks at day 14 as the fledging number (without our interference these chicks had 98.5% chance of fledging, after surviving to d 14 – only 14/918 chicks did not fledge).

Fledging success (SFL), proportion of chicks fledged to hatchling number per nest (fledgling number/hatchling number; hatchling number calculated as in the case of HS).

Fledging date (FLD), a day in which all chicks left the nest (number of days from April 1st).

Nesting time (NST), is the time that chicks spent in the nest from hatching till fledging (in days, FLD - HD). We only analysed nesting time if we recorded actual HD (nests where HD was estimated from incubation or chick appearance were excluded from the analyses).

8. Environmental data collection and weather conditions in the two study years

To characterize the environmental conditions occurring during BT and GT reproductive season in Bielany Forest in 2018 and 2019 (the comparative part of our study), we collected data on microclimate within nests, food availability at the study sites and weather in the two study seasons. Since we did not have enough temperature and humidity data loggers to record all nests, we were not able to account for microclimate of each nest in our models. Consequently, we do not show microclimate analyses in this study but discuss them in detail in Sudyka et al., (in prep). Because our study area is located within a capital city, we also evaluated if noise and air pollution were uniform across the two sites and did not interfere in our study design. Details on environmental data collection are presented below:

i) Food availability

Food availability was assessed by frass fall collection (recorded as grams/m^2/day) – an indirect, but widely accepted method to evaluate availability of caterpillars (Wesołowski & Rowiński, 2014), which are the main nutrient source for tits developing in natural habitats [ca. 74% of nestling diet in BT (Wesołowski & Rowiński, 2014)]. Frass containers were made of thick A4 paper (at least 200g/m3) by bending the walls and stapling them together, with 4 holes at the corners (1 mm) to allow the water to flow out but without the risk of frass loss. We placed the collectors on the ground and secured them with a large nail to avoid random displacement. The area of one collector was ca. 352.5 cm^2 (23.5 x 15 cm). The containers are not durable and in case of heavy rain may get destroyed: we lost data from 30 containers out of 352 over the 2 years (missing/eaten by snails/moved/destroyed by rain). These containers are easy to make with low cost, so it is possible to set up many (large number of replicates at a site) without concerns about losses, which may be relevant in urban settings. Frass collectors were placed in 11 separate locations within a site (see Fig. 1); there were 22 collectors in total at one time. We selected the same tree species (an approximate representation of species composition in Bielany Forest: five hornbeams, three oaks and three acers per site) between the two sites to account for various tree-species phenology (leaf development across season) and specific habitat preferences of caterpillars. We placed the collectors in the same location, under the same tree each year (marked with GPS and a ribbon). We were interested in assessing food availability in May since this is when an expected peak of caterpillar presence occurs and the majority of tits feed their young during this month (only three nests hatched before placing the first collectors and 6 nests fledged after the last collectors were picked up across the two years). We collected frass every 4 days (we recorded the exact time of set up and collection of each collector). In 2018 and 2019, we placed the first collectors on the 3rd of May and collected the last round on the 4th of June (eight collection rounds, we missed the 1st collection round in BIE in 2018 - thus it started there on the 7th of May that year). In total, we had 158 frass samples in 2018 and 161 in 2019 ready for analyses (319 out of 352 initially set up collectors; data was missing if a collector got lost/destroyed in the field and in case of double/mistaken labelling). Frass was carefully transferred from the collectors into paper envelopes and transported to the lab for weighing. All samples were weighed in May and June 2019 in random order by the same person. Briefly, the whole content of an envelope was transferred onto a petri dish and dried in 60 °C overnight. After drying, the content of the petri dish was cleaned from debris. To remove large debris (leaves, dead insects etc.), we used an analytical sieve with 2 mm mesh. If the content presented considerable amount of tiny plant material, we used a glass slide (smooth glass fragment placed at ca. 30° angle slope) to filter it out, since frass rolls down and the plant material remains stuck on the glass. We removed the rest of unwanted content under binoculars with tweezers and weighed the cleaned frass to the nearest 0.0001 g. The obtained frass mass was then extrapolated to a surface collection area of 1 m^2 (dividing frass mass by the area of the collector) and normalized to the exact number of days a collector was placed in the field (calculated from recorded times of set up and collection; mean 3.99 ± 0.1 days, range 3.68 – 4.44; in 20 cases we did not record the hour so we assumed 4.0 days in these cases). As a result, we obtained frass mass for each sample in $g/m^2/day$. The value was transformed as sqrt for normality and Z-score scaled for clarity of estimates. Food availability was uniform between the natural-cavity and nest-box sites but it was lower in 2019, and the timing of peak food availability differed between years, with a high peak of caterpillars occurring in the first week of May in 2018, and a much lower peak recorded in the fourth week of May in 2019. There was a tendency for greater food availability in the vicinity of oaks when compared to other tree species (Model S1, Fig. S1).

ii) Weather

We downloaded publicly available weather data from Bielany weather station, located within ca. 1.5 km from the core of the study area (https://danepubliczne.imgw.pl/data/dane_pomiarowo_obserwacyjne/) and compared daily values for: temperature (average, maximum and minimum), wind (average speed [m/s]), humidity (as % relative humidity) and rain (sum of precipitation [mm]) across the two study years, from March till July. The weather in 2019 was less favourable and unstable in comparison to 2018 (all model estimates in Models S2 below). March was much warmer in 2019 (a cue for earlier onset of reproduction), but April and May were significantly colder in terms of temperature average, minimum and maximum (Fig. S2 A-C, Models S2 A-C). These are the months that are critical for tit reproduction, as they directly impact vegetation and food base development, and consequently we observed delayed and decreased caterpillar peak in 2019 (Fig. S1). In 2019, April and June tended to be dryer (in terms of sum of precipitation and relative humidity: Fig. S2 D-E, Models S2 D-E) but May (the key month for nestling feeding) tended to be more humid with higher precipitation; additionally, 2019 tended to be more windy (Fig. S2 F, Model S2 F).

iii) Noise and air pollution

We recorded noise and air pollution at the same occasions, with portable measuring devices carried simultaneously by two people (one in BIB, one in BIE), who followed a track that covered the entire area of each study site. The measurements were taken in June 2018 on 4 separate days (2 weekend days and 2 workdays), three times per day (starting at 7:00 am, 12:00 am and 5:00 pm), thus we had 12 measurements per point (noise) or area (pollution). Each time the person followed the same track (the direction of the track was altered at every measurement round).

Noise was taken at 10 nest-boxes (total N = 120) and 10 cavities (total N = 120) randomly selected on the track. Air pollution was measured continuously on the entire track (e.g. we did not record the pollution at specific points, but we obtained average and maximum values per site). Noise pollution was measured with a portable Digital Sound Level Meter SL-200 (range: 30-130 dB; precision ± 1.5 dB; resolution 0.1 dB). It can measure sound in two modes dBA and dBC. Filter A applies to the mid-range frequencies (an approximation of human hearing) widely adopted for environmental noise measurement, while the dBC filter measures low and high frequencies (optimal for measuring impulsive noise). We took measurement in the SLOW mode to record constant sound levels and since the sound levels were always in the range 30 – 100 dB, we used the LOWER recording range. The measurements were done at the nest entrance and lasted for 5 seconds for each of the two scales, within which time we recorded the maximum sound level. Apart from not detecting differences between study sites (BIE and BIB, Model S3A and B), mid-range noise increased during afternoon rush hours on workdays (17:00, closeness of a major road Wisłostrada from the NE, Fig. 1, significant hour * weekday interaction, Fig. S3A), while impulsive noise was higher at midday (12:00, Fig. S3B).

Air pollution was measured by a real-time particulate matter recorder AirBeam, which allows to record average and maximum concentration (in µg/m^3) of PM 2.5 (fine particles, with a diameter of 2.5 µm or less). The device was connected via Bluetooth to a mobile phone and the data recorded with AirCasting app, which is an open-source environmental data visualization platform. Average pollution tended to be higher during workdays (Model S3 C, Fig. S3C), while its maximum value only at workdays during afternoon rush hour (17:00, significant hour * weekday interaction, Model S3D, Fig. S3D).

9. Statistical Analyses

Environmental variables. To test if food availability differed across study sites (BIE and BIB) and years, we used a linear mixed model with square root-transformed frass mass (to achieve normal distribution of residuals) as response variable. Site, year, tree species under which the collector was placed, sampling event and year * sampling event interaction were fitted as fixed categorical explanatory variables. Frass sampling point ID was fitted as a random effect.

To test for differences in weather conditions in the two study seasons, we introduced temperature (average, maximum and minimum), wind, humidity and rain (sqrt transformed to achieve a normal distribution of residuals) as responses in separate GLMs. Year, month and their interaction were fitted as fixed categorical explanatory variables.

To compare noise pollution between the sites, we fitted two measures: mid-range noise (dBA) and impulsive noise (dBC) as responses in two separate linear mixed models with site, weekday (weekend or workday), hour and all their interactions as explanatory fixed variables and sampling point ID as a random effect. Air pollution was tested with two GLMs fitting average and maximum concentration of PM 2.5 as a response and site, weekday and hour and their interactions as explanatory fixed variables.

Breeding densities, nest-box occupancy and failure rates. For each species, we calculated overall breeding densities as the maximum number of nests active at the same time (first clutches), separately in the core area of the natural-cavity plot and for the nest-box plot (Fig. 1). To test if tit nest-box occupancy rate differed between seasons, we employed a binomial GLM, with occupancy fitted as response variable (yes: 1 or no: 0). Study year and nest-box exposition [nest-box entrance facing one of the 8 cardinal and intercardinal directions; noted as important nesting parameter for some species (Ardia et al., 2006; Rendell & Robertson, 1994)] as categorical predictors. Both species were pooled in this analysis, since they were competing for and occupying the same pool of nest-boxes. Moreover, such approach allowed to include nests abandoned too early to differentiate which tit species occupied it (e.g. before egg laying stage). We also tested if the proportion of known species in occupied boxes differed between years using a $\chi2$ test. To determine if there are differences in nesting failure rate (no chick fledged) between natural-cavities and nest-boxes, we coded 1 if at least one chick fledged and 0 for a loss, and fit it as a response in a binomial GLM. We introduced nest type (understood as nesting site type: natural-cavity vs nest-box), nest exposition and year as fixed factors. Next, within nests that failed, we investigated reasons for losses in natural-cavities and nest-boxes using multinomial regression (within five categories of reasons/stages of loss: deserted at nest building, at egg laying/incubation, after hatching, predation and collapsing/flooding) and fitting nest type and year as fixed terms (since nest exposition ultimately did not influence nesting failure rate: Model S5, we did not account for it). In both analyses, we did not account for species for the following reasons: (i) at early nesting stages we did not know the species in several nest-boxes, (ii) the number of losses was relatively small (63 failures out of total 202 nests with known fledging success across 2 years, that is overall 31.2% of losses) - thus sample sizes in some categories of reasons of loss were low even when both species were investigated together (Fig. 2), and finally (iii) some reasons for nesting loss, such as nest collapsing or flooding, are species-independent. In both models, we checked for interactions between the main terms, but removed them if insignificant ($P > 0.05$). Importantly, subsequent analyses of life-history traits were performed separately for each species.

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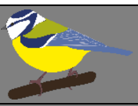
TABLES

Table S1. Basic parameters for BT and GT nests in all natural-cavities and nest-boxes in the two study seasons

Nest 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 [cm^2]	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	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 [cm^2]	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 [cm^3]	1883.2 (551.3-15833.6)	42	923.7(673.7-1041.1)	46	278.0	**<0.001**	3502.1 (289.0-41888.1)	57	959.5 (826.8-1133.0)	28	161.0	**<0.001**

All measurements were done according to the methodology in Maziarz et al., (2016) and Wesołowski & Rowiński, (2012).

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*1/2entrance width*1/2entrance 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.

Table S2. Occupancy in 65 nest-boxes. In parentheses number of second clutches are shown. In the column "Tit": number of nests abandoned too early to differentiate which tit species occupied it.

Year	**Blue tit** 	**Great tit** 	**Tit**	**Total**
2018	23	19	7	49
2019	23 (1)*	10 (2)	4	37(3)

*Includes two BT nests in the same nest-box, after desertion at egg laying.

Table S3. Supplementary information to the main analyses presented in Table 1. Estimates for lay date, its quadratic effect and interactions ± SE and Pr(> χ^2). If significant ($P < 0.05$), marked in bold.

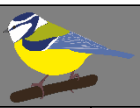
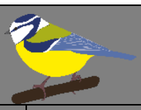
Model from Table 1	**Blue tits** 						**Great tits** 					
	Lay Date		Lay Date ^{2}		Interaction		Lay Date		Lay Date ^{2}		Interaction	
	Estimate ± SE	Pr(> χ^2)	Estimate ± SE	Pr(> χ^2)	Estimate ± SE	Pr(> χ^2)	Estimate ± SE	Pr(> χ^2)	Estimate ± SE	Pr(> χ^2)	Estimate ± SE	Pr(> χ^2)
Clutch Size	**-0.538 ± 0.097**	**<0.0001**					-0.161 ± 0.124	0.195				
Incubation Start	**1.941 ± 0.533**	**0.0003**	**-1.640 ± 0.502**	**0.001**			**0.018 ± 0.131**	**0.0003**			**nest type * LD: 0.713 ± 0.191**	**0.0002**
Hatch Rate	-1.991 ± 0.768	0.295			**nest type * LD: 2.170 ± 0.859**	**0.004**	-0.397 ± 0.439	0.781			**nest type * LD: 2.241 ± 1.151**	**0.020**
Hatching Success	0.052 ± 0.173	0.758					0.310 ± 0.228	0.169				
Hatching Date	**0.952 ± 0.032**	**<0.0001**					0.050 ± 0.320	0.877	**0.888 ± 0.318**	**0.005**		
Fledgling number	-0.202 ± 0.111	0.070					0.054 ± 0.139	0.697				
Fledging success	-0.140 ± 0.214	0.514					**0.642 ± 0.305**	**0.029**				
Fledging Date	**0.956 ± 0.041**	**<0.0001**					-0.306 ± 0.624	0.624	**1.332 ± 0.667**	**0.046**		
Nesting Time	-0.022 ± 0.123	0.857					0.211 ± 0.249	0.202			**year * LD: -0.645 ± 0.315**	**0.040**

Table S4. Sample sizes for main analyses of nests monitored in natural-cavities and in nest-boxes study sites and number of birds in the study

Sample size	Blue tit 					Great tit 				
	2018		2019		Total	2018		2019		Total
	Natural-cavity	Nest-box	Natural-cavity	Nest-box		Natural-cavity	Nest-box	Natural-cavity	Nest-box	
Nests	39	23	48	23	**133**	41	19	47	10	**117**
Lay date	18	23	24	23	**88**	20	18	24	10	**72**
Clutch size	16	21	19	18	**74**	19	17	20	10	**66**
Incubation start	10	20	13	16	**59**	16	17	15	10	**58**
Hatch rate	31	23	35	23	**112**	33	18	31	10	**92**
Hatching success	7	21	12	18	**58**	14	16	13	10	**53**
Hatching date	18	21	21	19	**79**	30	16	20	10	**76**
Fledgling number	12	21	21	18	**72**	21	16	20	9	**66**
Fledging success	7	21	14	18	**60**	14	16	15	9	**54**
Fledging date	14	20	18	14	**66**	22	15	16	9	**62**
Nesting time	12	20	18	14	**64**	18	15	14	9	**56**
Adult number	F 11 M 13	F 20 M 20	F 18 M 18	F 13 M 11	**F 62** **M 62**	F 21 M 18	F 14 M 15	F 18 M 14	F 10 M 9	**F 63** **M 56**
Chicks day 14	96	169	134	75	**474**	124	124	87	61	**396**
All chicks	110	192	162	167	**631**	143	150	118	65	**476**

All variables explained in the paragraph ‘Variables for analyses’ above.

Table S5. Basic life-history and fitness data of breeding events recorded in natural-cavities and nest-boxes located in the nest-box site (BIB) and natural-cavities in the natural-cavity site (BIE) in 2019

Nest Data	**Blue tits** 						**Great tits** 					
	Natural (BIB)		Nest-boxes (BIB)		Natural (BIE)		Natural (BIB)		Nest-boxes (BIB)		Natural (BIE)	
	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N
Lay date	15.7 ± 7.23	3	13.78 ± 10.04	23	14.0 ± 5.46	24	19.2 ± 5.00	4	18.3 ± 5.33	10	18.7 ± 4.87	24
Clutch size	9.3 ± 1.16	3	9.8 ± 2.13	18	10.6 ± 1.39	19	**11.0 ± 1.41**	**4**	**8.2 ± 1.03**	**10**	**8.8 ± 1.80**	20
Hatch rate	0.67 ± 0.52	6	0.83 ± 0.39	23	0.82 ± 0.39	34	0.86 ± 0.38	7	1.0 ± 0.00	10	0.81 ± 0.40	32
Hatching date	32.5 ± 0.70	2	37.0 ± 8.74	19	37.0 ± 4.93	21	41.0 ± 3.39	5	38.5 ± 4.77	10	38.8 ± 5.14	20
Fledgling number	4.0 ± 6.93	3	4.31 ± 3.52	16	6.4 ± 3.25	19	4.5 ± 3.42	4	6.0 ± 1.73	9	5.1 ± 3.27	19
Fledging success	0.0 ± 0.0	2	0.47 ± 0.38	18	0.60 ± 0.40	13	0.50 ± 0.71	2	0.83 ± 0.22	9	0.56 ± 0.42	14
Fledging date		0	56.2 ± 8.28	14	56.9 ± 4.87	18	57.3 ± 2.08	3	56.9 ± 3.72	9	57.6 ± 3.31	16
Nesting time		0	20.1 ± 1.00	14	19.3 ± 1.33	18	19.0 ± 0.00	2	19.3 ± 1.41	9	18.7 ± 1.98	14
Success rate*	0.20 ± 0.45	5	0.61 ± 0.50	23	0.61 ± 0.50	31	**0.57 ± 0.54**	**7**	**1.00 ± 0.00**	**10**	**0.55 ± 0.51**	**33**
Chick body mass	**11.0 ± 0.56**	**11 (1)**	**10.7 ± 1.02**	**79 (14)**	**11.1 ± 0.83**	**134 (18)**	**14.5 ± 1.39**	**8 (2)**	**16.5 ± 1.19**	**61 (10)**	**15.8 ± 1.64**	**87 (14)**
Chick tarsus	16.8 ± 0.44	11 (1)	16.7 ± 0.70	79 (14)	16.9 ± 0.67	134 (18)	19.7 ± 0.88	8 (2)	19.6 ± 0.68	61 (10)	19.4 ± 0.78	87 (14)
Chick body condition**	0.08 ± 0.50	11 (1)	-0.22 ± 1.21	79 (14)	0.12 ± 0.87	134 (18)	**-1.5 ± 1.37**	**8 (2)**	**0.28 ± 0.82**	**61 (10)**	**-0.06 ± 0.95**	**87 (14)**

All variables are defined in the paragraph "Variables for analyses" above. Significant differences among the 3 nest types according to Kruskall-Wallis test (P < 0.05) are highlighted in bold. We do not show data for adults since there was only one BT male and one female and one GT male and one female from natural-cavities in BIB. For chick data, the number of nests is reported in parentheses in the "N" column. * Ratio of nests with successfully fledged young (at least 1) to all nests; **Calculated as residuals from body mass over tarsus regression.

FIGURES

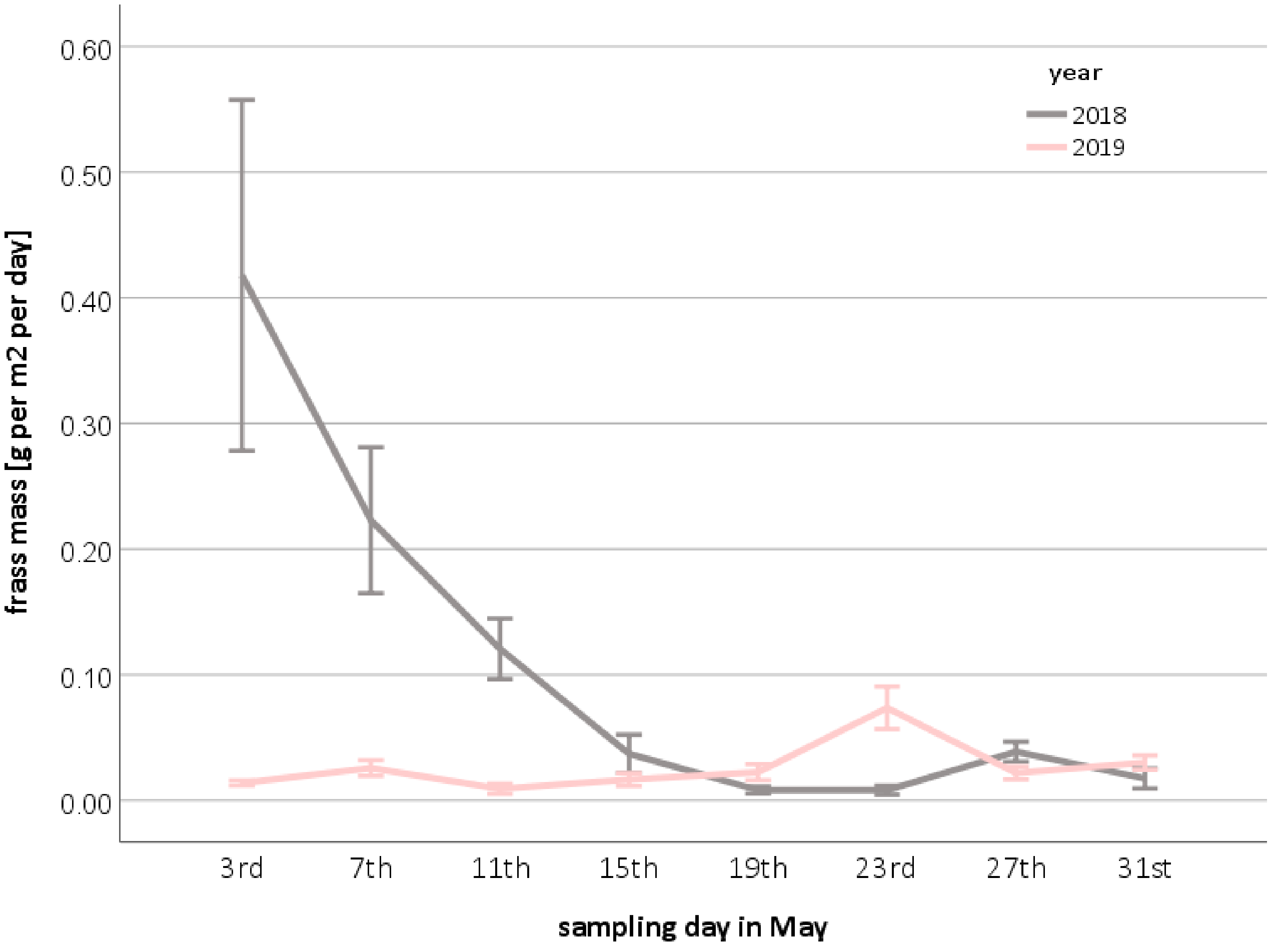
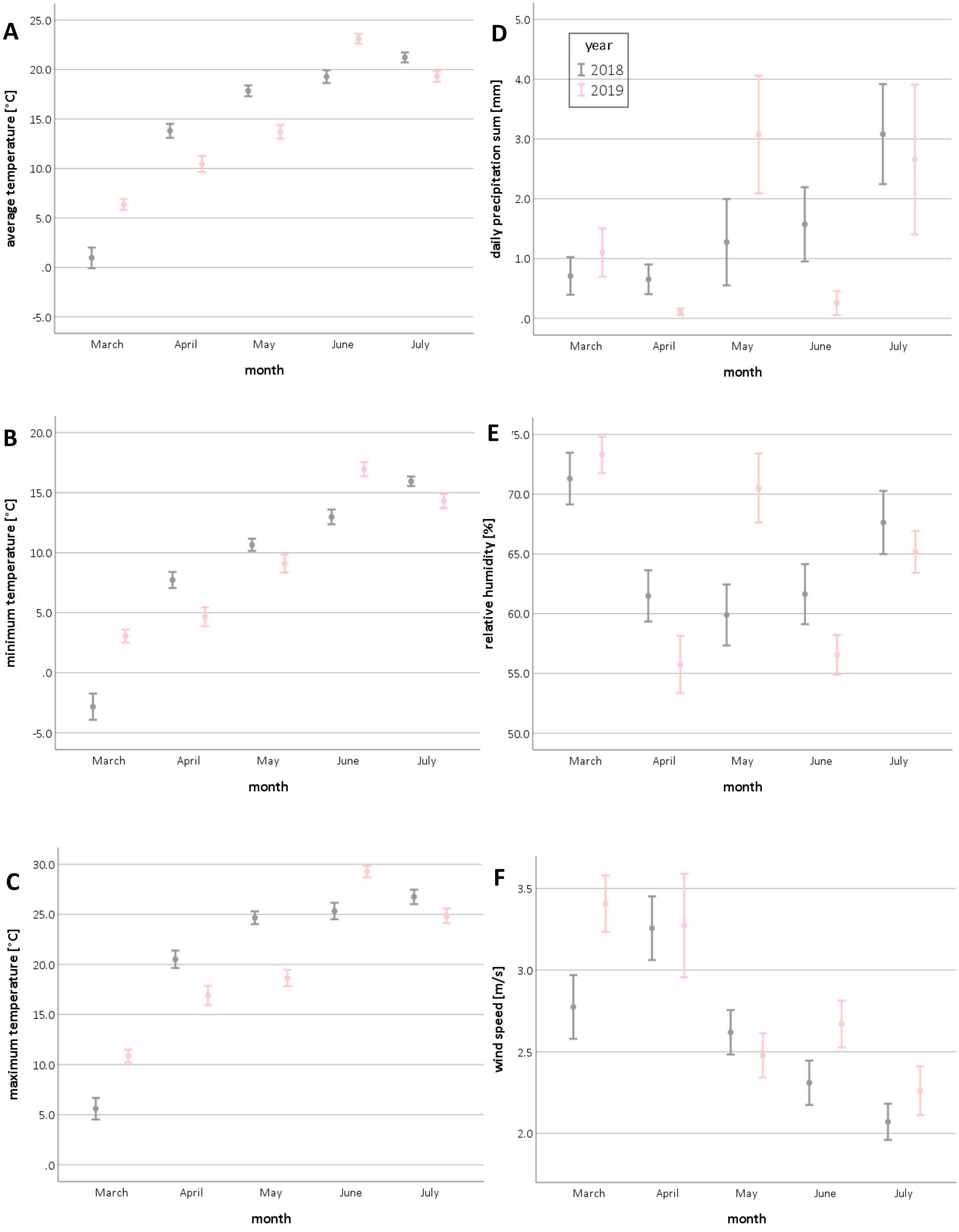


Fig. S1 Food availability as average frass mass per sampling occasion (grams/m^2/day), raw data without transformations are shown ± SE.

Fig. S2 (next page). Weather components in the two study years. Graphs show raw data means ± SE. A) average daily ambient temperature; B) minimum daily ambient temperature; C) maximum daily ambient temperature; D) daily sum of precipitation; E) relative humidity; F) average daily wind speed (interaction year * month was not significant but we show it for consistency of data presentation).


A
average temperature [°C]
25.0
20.0
15.0
10.0
5.0
.0
-5.0
March
April
May
June
July
month
D
daily precipitation sum [mm]
year
2018
2019
5.0
4.0
3.0
2.0
1.0
.0
March
April
May
June
July
month
B
minimum temperature [°C]
20.0
15.0
10.0
5.0
.0
-5.0
March
April
May
June
July
month
E
relative humidity [%]
5.0
70.0
65.0
60.0
55.0
50.0
March
April
May
June
July
month
C
maximum temperature [°C]
30.0
25.0
20.0
15.0
10.0
5.0
.0
March
April
May
June
July
month
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March
April
May
June
July
month

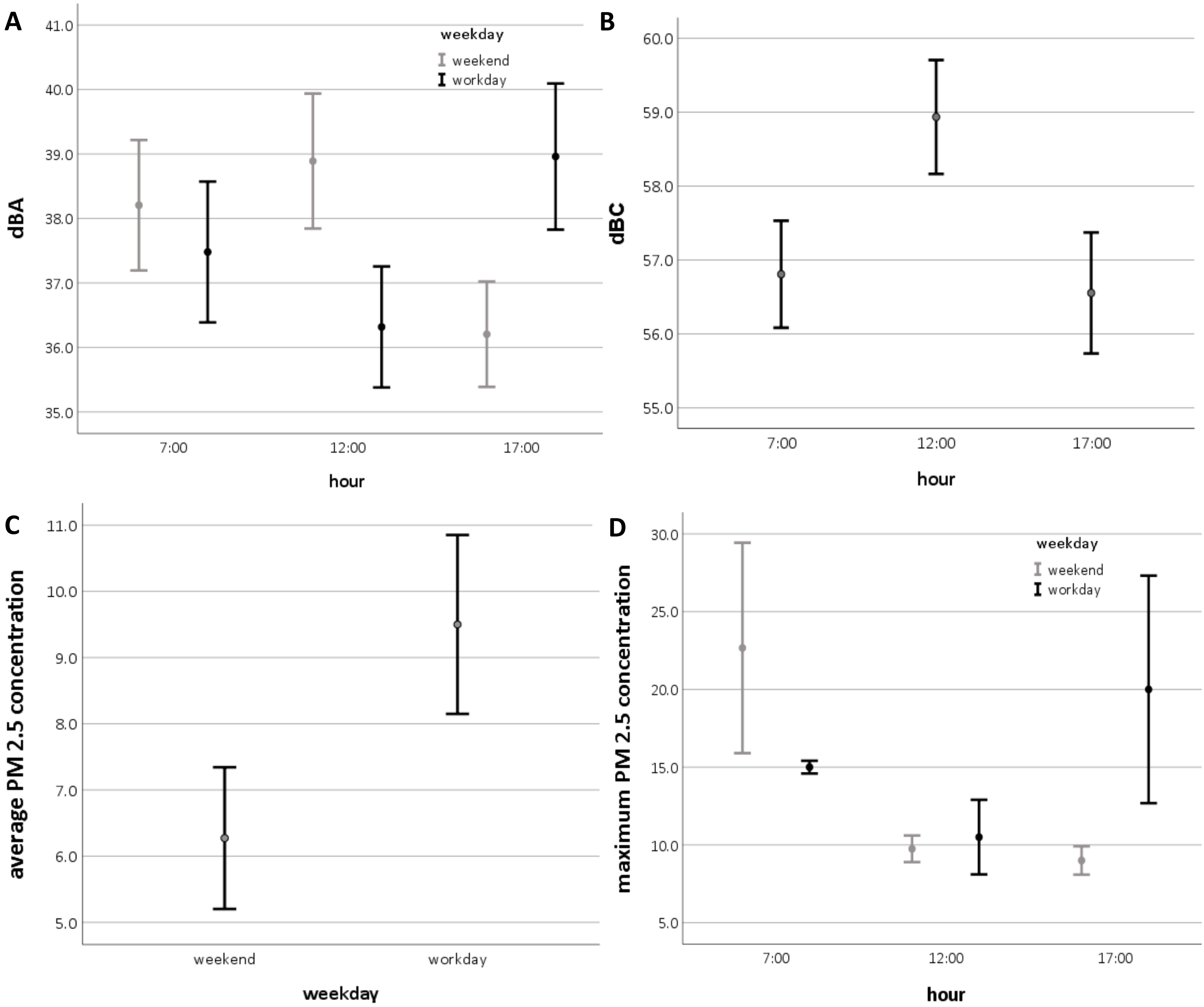

Fig. S3 Anthropogenic disturbance components in the study sites. Graphs show raw data means ± SE**.** Noise pollution: A) mid-range noise (dBA); B) impulsive noise (dBC). Air pollution: C) average and D) maximum concentration of PM 2.5.

MODELS

Model S1 Linear mixed models for explaining food availability (measured as caterpillar frass mass). Natural-cavity site (BIE), year 2018, oaks and sampling performed on the 3rd of May are used as references for parameter estimates. Significant differences ($P < 0.05$) are indicated in bold, trends ($P < 0.2$) in italics.

Variable		**χ^2**	**df**	**Pr(> χ^2)**	**Estimate ± SE**
site		0.992	1,18	0.319	
	nest-box (BIB)				0.170 ± 0.171
year		**43.564**	**1,282**	**<0.0001**	
	2019				-2.508 ± 0.235
sampling event		**112.957**	**7,282**	**<0.0001**	
	7th May				-0.744 ± 0.231
	11th May				-1.291 ± 0.233
	15th May				-2.234 ± 0.237
	19th May				-2.762 ± 0.235
	23rd May				-2.793 ± 0.233
	27th May				-2.098 ± 0.231
	31st May				-2.552 ± 0.231
tree species		*5.306*	*2,18*	*0.07*	
	acer				-0.515 ± 0.231
	hornbeam				-0.358 ± 0.207
year*sampling event		**234.951**	**7,282**	**<0.0001**	
	2019 * 7th May				0.952 ± 0.304
	2019 *11th May				1.082 ± 0.303
	2019 *15th May				2.166 ± 0.312
	2019 *19th May				2.822 ± 0.308
	2019 *23rd May				3.568 ± 0.301
	2019 *27th May				2.265 ± 0.303
	2019 *31st May				2.864 ± 0.302

Variance for the random effects frass sampling point ID: 0.133 and residual: 0.382.

Models S2 General linear models of weather components between March and July in the two study years. We retain and present the interaction of the two main factors only if significant. March and 2018 are the references for the estimates and all estimates are shown after Z-score scaling of continuous variables:

A) average daily ambient temperature, B) minimum daily ambient temperature, C) maximum daily ambient temperature, D) daily sum of precipitation (sqrt transformed for normality), E) relative humidity and F) average daily wind speed. Significant differences ($P < 0.05$) marked in bold, trends ($P < 0.2$) in italics.

Model	Variable		χ^2	df	Pr(> χ^2)	Estimate ± SE
A) average daily ambient temperature	year		0.01	1,304	0.916	
		2019				0.707 ± 0.124
	month		**893.60**	**4,300**	**<0.0001**	
		April				1.683 ± 0.125
		May				2.212 ± 0.124
		June				2.400 ± 0.125
		July				2.654 ± 0.124
	year*month		**83.40**	**4,296**	**<0.0001**	
		2019 * April				-1.148 ± 0.177
		2019 * May				-1.250 ± 0.176
		2019 * June				-0.205 ± 0.177
		2019 * July				-0.958 ± 0.176
B) minimum daily ambient temperature	year		*2.86*	*1,304*	*0.091*	
		2019				0.838 ± 0.136
	month		**700.27**	**4,300**	**<0.0001**	
		April				1.504 ± 0.137
		May				1.921 ± 0.136
		June				2.252 ± 0.137
		July				2.675 ± 0.136
	year*month		**67.70**	**4,296**	**<0.0001**	
		2019 * April				-1.274 ± 0.194
		2019 * May				-1.060 ± 0.192
		2019 * June				-0.271 ± 0.194
		2019 * July				-1.072 ± 0.192
C) maximum daily ambient temperature	year		0.87	1,304	0.352	
		2019				0.628± 0.134
	month		**722.79**	**4,300**	**<0.0001**	
		April				1.782 ± 0.135
		May				2.277 ± 0.134
		June				2.357 ± 0.135
		July				2.526 ± 0.134
	year*month		**74.53**	**4,296**	**<0.0001**	
		2019 * April				-1.059 ± 0.191
		2019 * May				-1.347 ± 0.190
		2019 * June				-0.157 ± 0.191
		2019 * July				-0.853 ± 0.190

Model	Variable		χ^2	df	Pr(> χ^2)	Estimate ± SE
D) daily sum of precipitation	year		0.037	1,304	0.848	
		2019				0.145 ± 0.245
	month		**21.618**	**4,300**	**0.0002**	
		April				0.003 ± 0.247
		May				0.049 ± 0.245
		June				0.190 ± 0.247
		July				0.624 ± 0.245
	year*month		**11.458**	**4,296**	**0.022**	
		2019 * April				-0.437 ± 0.349
		2019 * May				0.465 ± 0.346
		2019 * June				-0.589 ± 0.349
		2019 * July				-0.291 ± 0.346
E) relative humidity	year		0.002	1,304	0.965	
		2019				0.145 ± 0.233
	month		**49.828**	**4,300**	**<0.0001**	
		April				-0.716 ± 0.235
		May				-0.833 ± 0.233
		June				-0.705 ± 0.235
		July				-0.268 ± 0.233
	year*month		**17.693**	**4,296**	**0.001**	
		2019 * April				-0.564 ± 0.332
		2019 * May				0.630 ± 0.329
		2019 * June				-0.517 ± 0.332
		2019 * July				-0.324 ± 0.329
F) average daily wind speed	year		*3.549*	*1,304*	*0.060*	
		2019				0.200 ± 0.106
	month		**52.046**	**4,300**	**<0.0001**	
		April				0.164 ± 0.168
		May				-0.510 ± 0.166
		June				-0.566 ± 0.168
		July				-0.870 ± 0.166

Models S3 Linear mixed models of noise pollution: A) mid-range noise (dBA); B) impulsive noise (dBC) and general linear models of air pollution: C) average and D) maximum concentration of PM 2.5. We retain and present the interaction of the two main factors only if significant. Natural-cavity site (BIE), hour 9:00 and weekend are the references for the estimates and all estimates are shown after Z-score scaling of continuous variables. Significant differences ($P < 0.05$) marked in bold, trends ($P < 0.2$) in italics.

Model	Variable		χ^2	df	Pr(> χ^2)	Estimate ± SE
A) mid-range noise (dBA)	site		1.565	1,18	0.211	
		BIB				0.300 ± 0.239
	hour		0.105	2,215	0.949	
		12:00				0.107 ± 0.196
		17:00				-0.311 ± 0.196
	weekday		0.062	1,215	0.803	
		workday				-0.113 ± 0.196
	hour * weekday		**9.244**	**2,215**	**0.010**	
		12:00 * workday				-0.287 ± 0.277
		17:00 * workday				0.541 ± 0.277
B) impulsive noise (dBC)	site		0.175	1,18	0.675	
		BIB				-0.108 ± 0.257
	hour		**7.607**	**2,217**	**0.022**	
		12:00				0.306 ± 0.136
		17:00				-0.036 ± 0.136
	weekday		0.0001	1,217	0.992	
		workday				-0.001 ± 0.111
C) average concentration of PM 2.5	site		0.012	1,21	0.912	
		BIB				-0.043 ± 0.385
	hour		*4.305*	*2,19*	*0.116*	
		12:00				-0.986 ± 0.477
		17:00				-0.617 ± 0.477
	weekday		*3.170*	*1,18*	*0.075*	
		workday				0.686 ± 0.385
D) maximum concentration of PM 2.5	site		1.318	1,18	0.251	
		BIB				0.431 ± 0.375
	hour		*4.389*	*2,19*	*0.111*	
		12:00				-1.586 ± 0.686
		17:00				-1.674 ± 0.686
	weekday		0.268	1,18	0.604	
		workday				-0.971 ± 0.686
	hour * weekday		*5.921*	*2,16*	*0.052*	
		12:00 * workday				1.059 ± 0.932
		17:00 * workday				2.260 ± 0.932

Variance for the random effects for dBA: sampling point ID: 0.222 and residual: 0.766; for dBC: sampling point ID: 0.269 and residual: 0.743.

Model S4 Binomial generalised linear model explaining nest-box occupancy rate. 2018 and East exposition are the references for parameter estimates. Significant differences (P < 0.05) are indicated in bold.

Variable		**χ^2**	**df**	**Pr(> χ^2)**	**Estimate ± SE**
year		**6.262**	**1,128**	**0.012**	
	2019				-0.977 ± 0.399
exposition		9.586	7,121	0.213	
	N				1.101 ± 0.712
	NE				0.932 ± 0.672
	NW				0.652 ± 0.687
	S				0.539 ± 0.826
	SE				<0.001 ± 0.738
	SW				-1.090 ± 0.987
	W				-0.357 ± 0.646

Model S5 Binomial generalised linear model of nesting failure. Natural-cavity, 2018 and East exposition are the references for parameter estimates. Significant differences (P < 0.05) are indicated in bold, trends (P < 0.2) are in italics.

Variable		**χ^2**	**df**	**Pr(> χ^2)**	**Estimate ± SE**
nest type		0.537	1,198	0.464	
	nest-box				-0.250 ± 0.341
year		**4.984**	**1,190**	**0.026**	
	2019				-0.741 ± 0.335
exposition		*9.586*	*7,191*	*0.094*	
	N				0.759 ± 0.571
	NE				0.902 ± 0.588
	NW				0.518 ± 0.584
	S				0.742 ± 0.774
	SE				-0.881 ± 0.627
	SW				-0.053 ± 0.653
	W				0.784 ± 0.617

Model S6 Multinomial regression for explaining reasons/stages of nesting failure. Natural-cavity and 2018 are the references for explanatory variables estimates and desertion at building for the estimates of the outcome variable. Significant differences ($P < 0.05$) are indicated in bold.

Variable		outcome	χ^2	df	Pr(> χ^2)	Estimate ± SE
nest type			**12.014**	**4**	**0.017**	
	nest-box	deserted at egg laying/incubation				-16.620 ± 0.543
		deserted after hatching				5.575 ± 0.604
		predation				-34.446 ± 0.548
		collapsing/flooding				-12.905 ± <0.001
year			3.394	4	0.494	
	2019	deserted at egg laying/incubation				-15.416 ± 0.451
		deserted after hatching				5.863 ± 0.604
		predation				-16.109 ± 0.686
		collapsing/flooding				13.360 ± 0.323
nest type * year			**10.526**	**4**	**0.032**	
	nest-box * 2019	deserted at egg laying/incubation				16.620 ± 0.827
		deserted after hatching				-4.477 ± 0.835
		predation				34.223 ± 0.548
		collapsing/flooding				-4.918 ± <0.001