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).

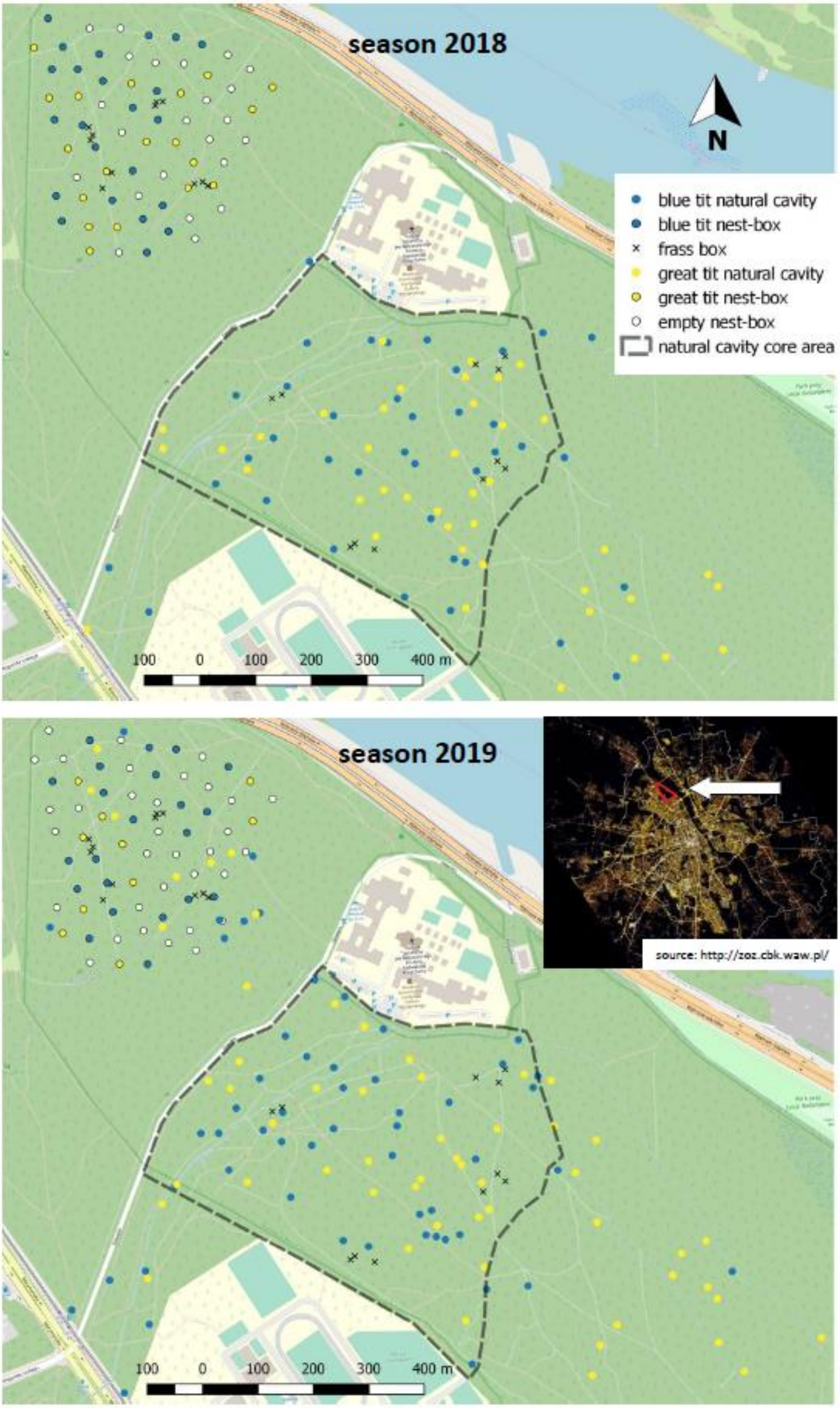

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Fig. 1 Map of the study sites with nest distribution in Bielany Forest in 2018 (top) and 2019 (bottom). The night-time photograph indicates the location of Bielany Forest in the Warsaw city matrix.

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 ($\chi^2 = 0.992$, $P = 0.319$). However, it was lower in 2019, and the timing of peak food availability differed between years, with a high peak of caterpillars occurring 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 ($\chi^2 = 1.565$, $P = 0.211$ and $\chi^2 = 0.175$, $P = 0.675$ respectively, Model S3A-B) and so was air pollution (both average and maximum concentration of PM 2.5, $\chi^2 = 0.012$, $P = 0.912$ and $\chi^2 = 1.318$, $P = 0.251$ 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).

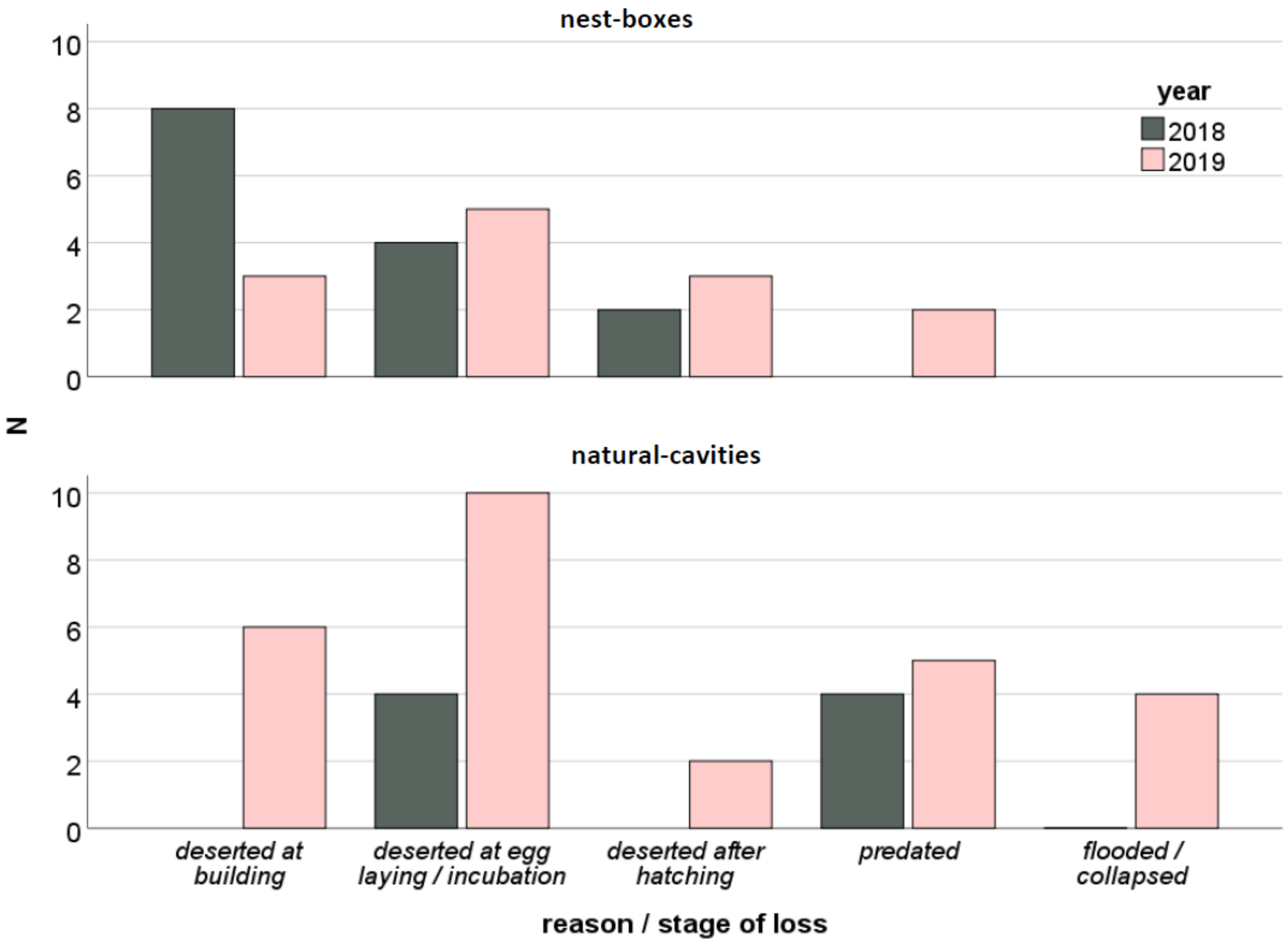

Fig. 2 Reasons/stages for nest losses in nest-boxes (top) and natural-cavities (bottom). Data from 86 nest-boxes (2018: 49, 2019: 37) and 115 natural-cavities (2018: 51, one case where female incubated an empty nest excluded, 2019: 64). Bars show number of cases.

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.

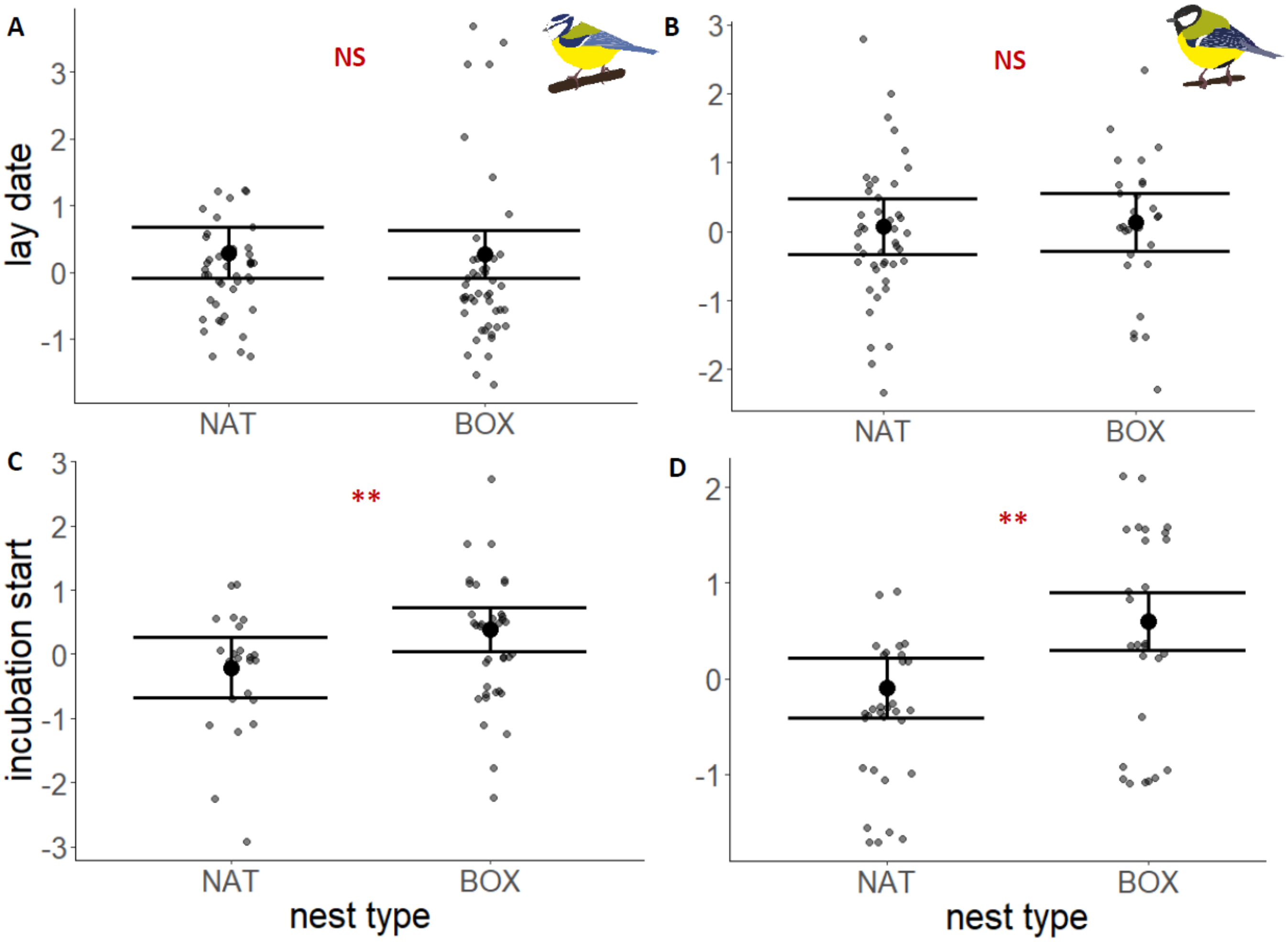

Fig. 3 Lay date (A-B) and incubation start (C-D) of blue tits (A, C) and great tits (B, D) breeding in natural-cavities (NAT) and nest-boxes (BOX) in Bielany Forest. Predicted values ± 95% CI are shown on Z-score scaled response variables in days. Significance levels for nest type: NS: not significant,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

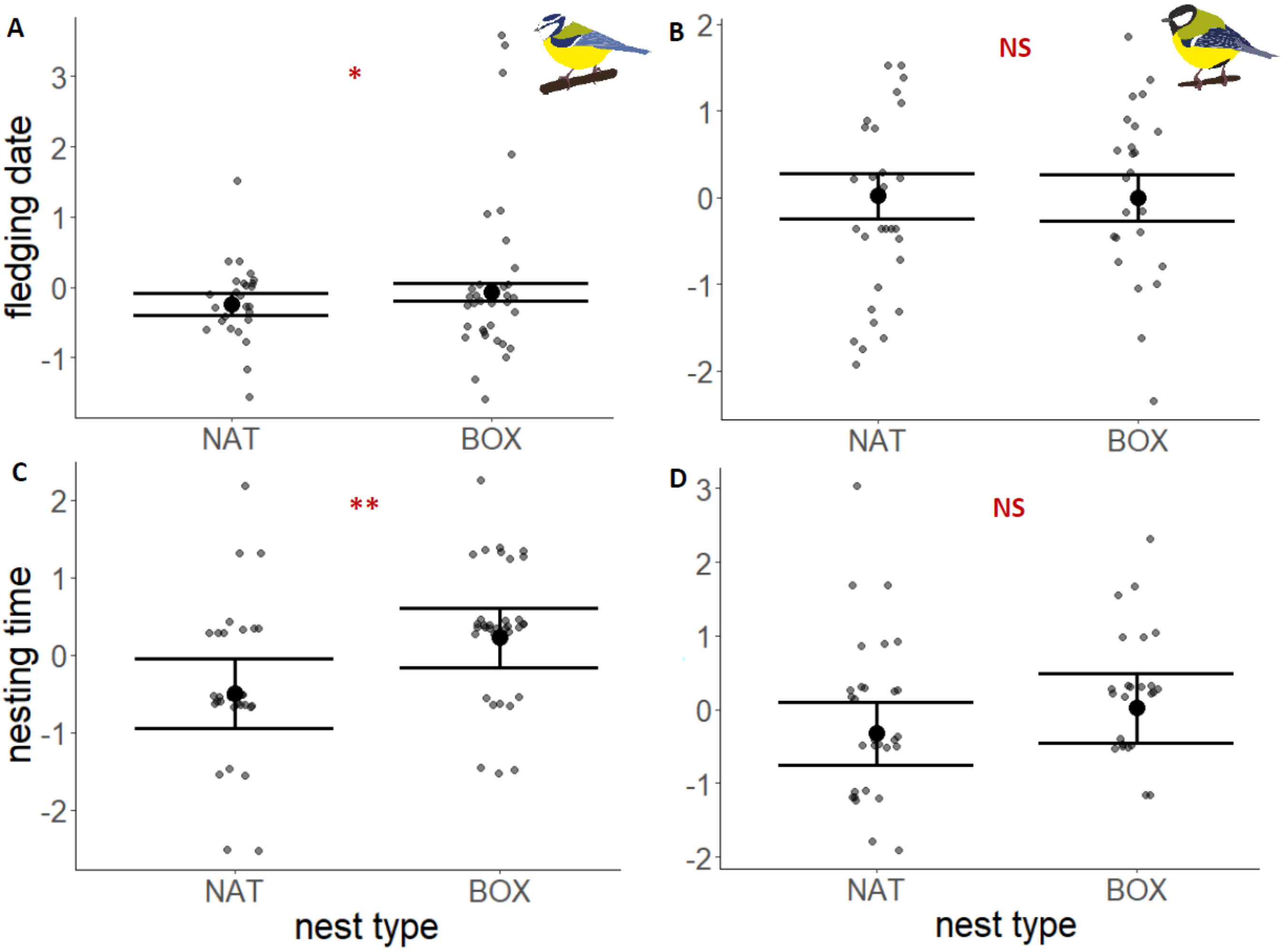

Fig. 4 Fledging date (A-B) and nesting time (the number of days from hatching till fledging; C-D) of blue tits (A, C) and great tits (B, D) breeding in natural-cavities (NAT) and nest-boxes (BOX) in Bielany Forest. Predicted values ± 95% CI are shown on Z-score scaled response variables in days. Significance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

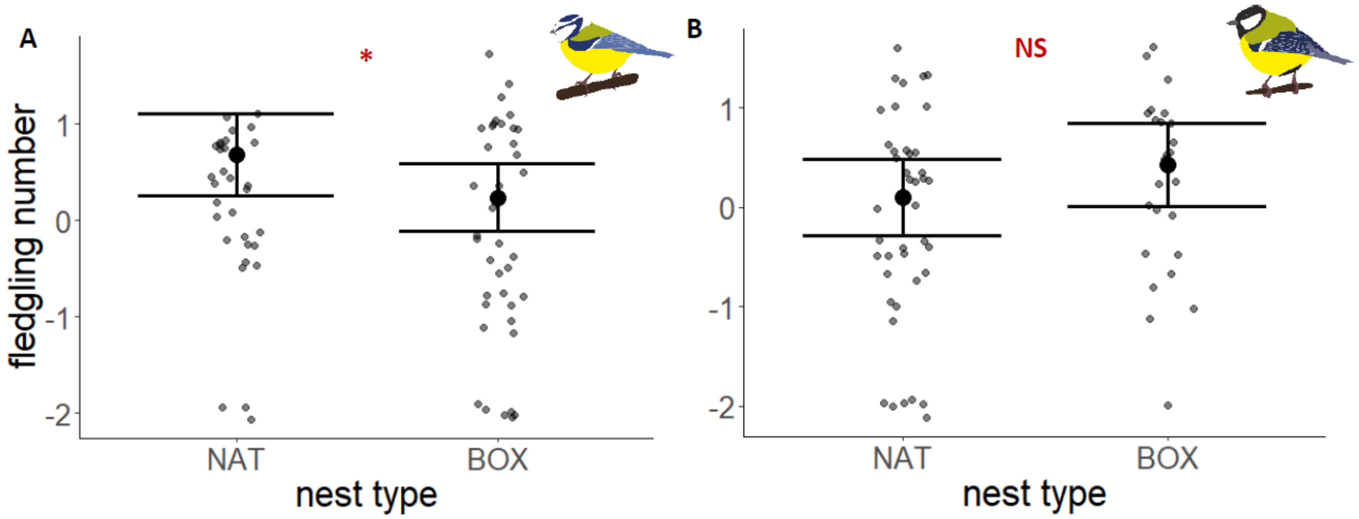

Fig. 5 Number of fledged young of blue tits (A) and great tits (B) breeding in natural-cavities (NAT) and nest-boxes (BOX) in Bielany Forest. Predicted values ± 95% CI are shown on a Z-score scaled response variable. Significance levels for nest type: NS: not significant, *: 0.01<P<0.05.

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.

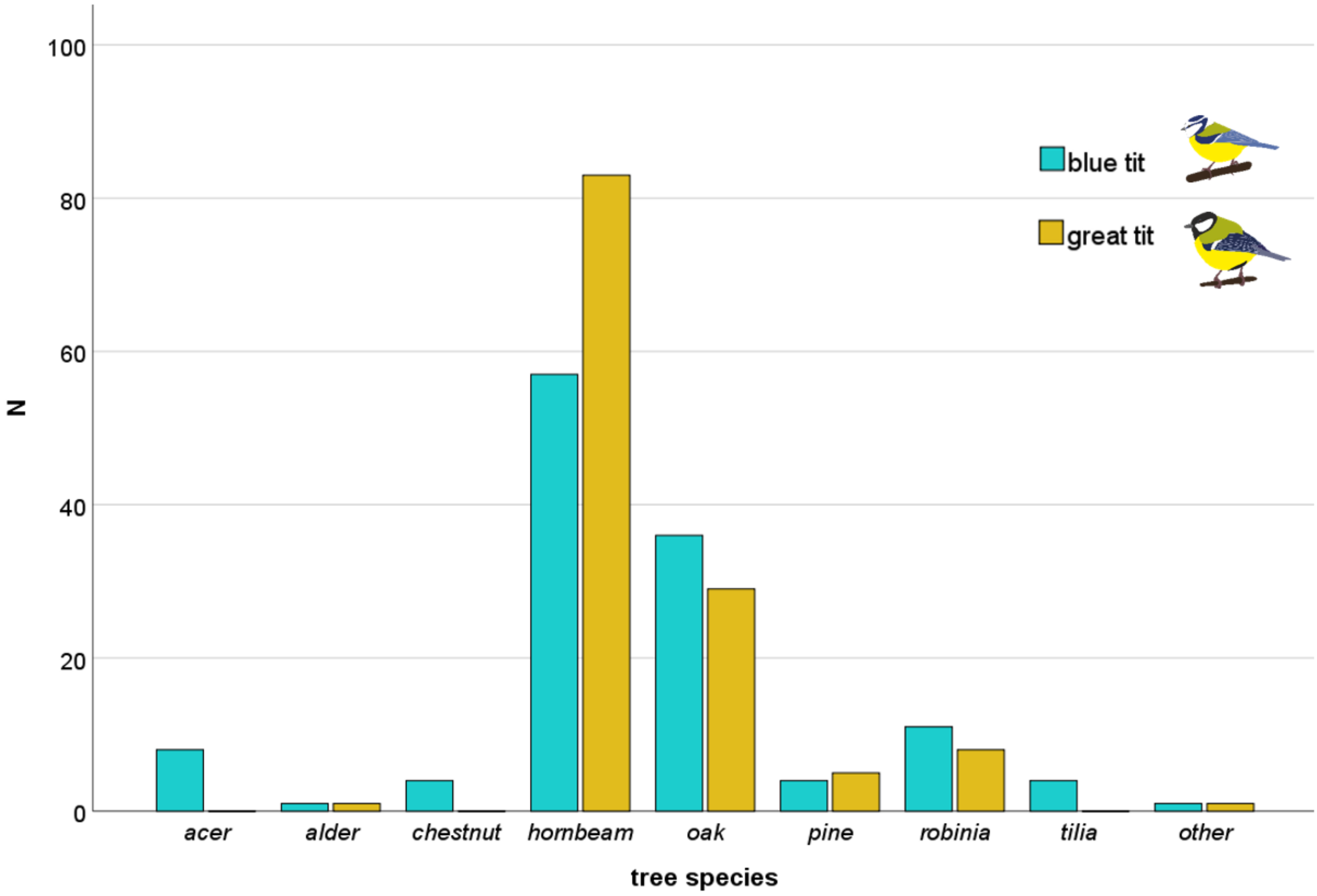

Fig. 6 Tree genera used by tits for nesting in natural-cavities in the three study seasons (2017-2019) in Bielany Forest. Bars show number of cases.

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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