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Double-brooding and annual breeding success of great tits in urban and forest habitats

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Abstract

Urban areas differ from natural habitats in several environmental features that influence the characteristics of animals living there. For example, birds often start breeding seasonally earlier and fledge fewer offspring per brood in cities than in natural habitats. However, longer breeding seasons in cities may increase the frequency of double-brooding in urban compared with nonurban populations, thus potentially increasing urban birds' annual reproductive output and resulting in lower habitat difference in reproductive success than estimated by studies focusing on first clutches only. In this study, we investigated 2 urban and 2 forests great tit *Parus major* populations from 2013 to 2019. We compared the probability of double-brooding and the total number of annually fledged chicks per female between urban and forest habitats, while controlling for the effects of potentially confounding variables. There was a trend for a higher probability of double-brooding in urban (44% of females) than in forest populations (36%), although this was not consistent between the 2 urban sites. Females produced significantly fewer fledglings annually in the cities than in the forest sites, and this difference was present both within single- and double-brooded females. Furthermore, double-brooded urban females produced a similar number of fledglings per season as single-brooded forest females. These results indicate that double-brooding increases the reproductive success of female great tits in both habitats, but urban females cannot effectively compensate in this way for their lower reproductive output per brood. However, other mechanisms like increased post-fledging survival can mitigate habitat differences in reproductive success.

Keywords: annual reproductive success, habitat differences, population self-sustainability, second brood, urban conservation

Urbanization can affect various demographic parameters of bird populations, which are important determinants of population growth and persistence and may also influence life-history strategies. Cities are often unfavorable habitats for the reproduction of birds (Sepp et al. 2017). For example, in several passerine species, smaller clutch size (Chamberlain et al. 2009; Caizergues et al. 2018), lower hatching success (Bailly et al. 2016a; Charmantier et al. 2017), and reduced body condition and survival of nestlings (Bańbura and Bańbura 2012; Bailly et al. 2016b; Seress et al. 2020) have been reported in urban compared with more natural habitats, resulting in a lower reproductive success per breeding attempt.

Although dozens of studies compared breeding success between urban and nonurban populations (reviewed by Chamberlain et al. 2009; Sepp et al. 2017), these typically focused only on seasonally first broods even in species that are known to have second broods frequently (Reale and Blair, 2005). Having multiple broods per breeding season is a widespread strategy in birds to increase their annual reproductive success (Naef-Daenzer et al. 2011; Hoffmann et al. 2015; Cornell and Williams 2016). Moreover, several features of

urban habitats may facilitate this strategy. For example, the advanced leaf emergence of urban plants (Neil and Wu 2006) can advance spring food availability, hence may result in seasonally earlier egg-laying in urban birds (Deviche and Davies 2014; Seress et al. 2018, but see: Bailly et al. 2016a), which in turn may increase the propensity of individuals to initiate seasonally second broods (Jackson and Cresswell 2017; Batey 2018). In nonmigratory passerines, the abundant human-provided winter food sources (e.g., bird feeders) and the generally milder winter climate in cities might also result in better post-winter body condition, potentially helping females to lay earlier and produce multiple clutches within a breeding season (Verhulst 1998; Galbraith et al. 2015; Glądalski et al. 2016; Pigeault et al. 2020). Consequently, the higher frequency of multiple broods per year may potentially compensate urban birds for their lower breeding success per breeding attempt or may even result in equivalent or higher annual reproductive output compared with their nonurban conspecifics (Reale and Blair, 2005; Muller et al. 2020).

Despite that, the frequency of double-brooding has important consequences both at the individual (lifetime reproductive

success) and the population (population dynamics) level, studies that compared the number of breeding attempts per year between urban and rural bird populations, are rare and their findings are equivocal. Some of the few studies that included multiple broods per female within a year found either no difference in the number of nesting attempts between urban and rural habitats (Batten 1973; Luniak et al. 1992; Leston and Rodewald 2006) or reported fewer (Luniak 1992; Rodewald and Shustack 2008) or a higher number of second clutches in cities (Cowie and Hinsley 1987). Accordingly, urbanization could affect the breeding habitat's features and so the probability of double-brooding in several positive and negative ways. To get a better understanding of the actual difference between urban and nonurban birds' reproductive success, we clearly need more information on how urbanization affects the frequency of double-brooding and the number of fledglings produced during the whole breeding season.

To fill this knowledge gap, here we analyzed breeding success data of a common urban adapter and facultative double-breeder species, the great tit (Del Hoyo et al. 2007). This species is a widespread model organism in urban ecology, especially in Europe, and several former studies showed the negative effects of habitat urbanization on clutch size (Wawrzyniak et al. 2015; Caizergues et al. 2018; Seress et al. 2018), hatching success (Bailly et al. 2016a; Charmantier et al. 2017), body condition, and nestling survival (Bailly et al. 2016b; Corsini et al. 2020; Seress et al. 2020). In this study, we investigated 2 urban and 2 forest populations over the course of 7 years and compared (1) the probability of double-brooding and (2) the number of annually produced fledglings per female between urban and forest habitats. Based on the earlier start of breeding in urban areas (Seress et al. 2018), we predicted a higher probability of double-brooding in urban vs. forest habitats, and therefore a smaller between-habitat difference in the number of annually fledged offspring per female than when we consider only the seasonally first broods.

Materials and Methods

Study sites and breeding biology

We studied great tits breeding in nest boxes at 2 urban and 2 forest sites in Hungary from 2013 to 2019. In one of the urban study sites, Veszprém (47°05′17.29″N, 17°54′29.66″E), the nest boxes were placed in public parks, a cemetery, and a bus station, where human activity, vehicle traffic, and noise pollution are typically intense. At this site, Norway maple *Acer platanoides* and European ash *Fraxinus excelsior* are the most common native tree species and horse chestnut *Aesculus hippocastanum* and black pine *Pinus nigra* are the most common non-native species. The average daily temperature (mean ± standard [SD]) during the breeding season (March 1–July 15) was 15.3 ± 1.85 °C.

In the other urban study site, Balatonfüred (46°57′30″N, 17°53′34″E), the nest boxes were placed in a park (ca. 9 ha) in the central part of the city, which is surrounded by an urban matrix with residential areas and roads with heavy traffic. The small-leaved lime *Tilia cordata*, the Norway maple, and the sessile oak *Quercus petraea* are the most common tree species and the black pine is the dominant non-native species. Balatonfüred has a somewhat warmer climate than Veszprém and the 2 forest study sites: the average daily temperature during the breeding season was 16.4 ± 1.19 °C.

The 2 forest sites were located in mature woodlands near Szentgál (47°06′39″N, 17°41′17″E) and at Vilma-puszta (47°05′06.7″N, 17°51′51.4″E), 2–3 km away from the nearest human settlement. Szentgál is a mixed beech *Fagus sylvatica* and hornbeam *Carpinus betulus* forest. The average daily temperature during the breeding season was 13.4 ± 1.51 °C. Human activity is relatively rare in the study area, although there is regular logging and hunting during some periods of the year. Vilma-puszta is a mature deciduous woodland characterized mainly by downy oak *Quercus cerris* and South European flowering ash *Fraxinus ornus*. The average daily temperature during the breeding season was 14.8 ± 1.47 °C. Vilma-puszta is a Natura 2000 site that is relatively free from human disturbance: it has no paved roads, there is only one nearby farm, and there is no logging activity; though it is occasionally visited by hunters. Both the Szentgál and Vilma-puszta sites represent common types of forests typical in Hungary (Borhidi 2003).

In total, there were 315–353 nest boxes at the 4 study sites available for the birds during the study period (see details in Supplementary Table S1). The number of nest boxes varied between years because a few nest boxes disappeared, or were removed, or relocated to new places (see Supplementary Table S1). We monitored a total of 100–233 great tit nests annually, depending on nest box occupancy.

We checked the nest boxes every 3 or 4 days from March to early July to record laying and hatching dates as well as the number of eggs and nestlings. When we found >1 egg during the first nest check, we back-calculated the first egg date by assuming that 1 egg was laid per day. We ringed each nestling at Day 14- to 16 post-hatch (i.e., a few days before fledging; hatching day of the first chick = Day 1) with a numbered metal ring, except in 2013 and 2014 when nestlings were also marked individually by 3 plastic color rings. Shortly after fledging (typically within a few days, up to 2 weeks, after ringing) we carefully examined the nest material to identify and count the number of chicks that died in the nest after the time of ringing. We calculated the number of successfully fledged young ("number of fledglings" henceforth) as the number of nestlings ringed minus the number of ringed nestlings found dead in the nest after ringing.

We captured most parent great tits in their nest box during brood rearing and marked each bird with a unique combination of 1 metal and 3 plastic color rings. A smaller number of adults was caught during the winter at feeder sites with mist nets. Upon capturing, we determined birds' sex and age based on their plumage characteristics and distinguished 2 age classes: first-year (FY) birds (hatched in the previous breeding season) and after FY (AFY) birds (having at least 1 breeding season before the current one). Nest boxes were equipped with a nontransparent plastic box that served as concealment for a small video camera. We video-recorded nests during the brood-rearing period and used these videos to individually identify color-ringed parents.

We included only those breeding attempts in the analyses in which at least 1 chick hatched because the identity of the female was often unknown in broods that failed during the egg-laying or incubation stage (see above). There was no difference between habitats in the number of failed nests during this stage (urban sites: 52 nests, forest sites: 50 nests; chi-squared test of the habitat difference in the number of failed vs. not failed clutches: $\chi^2 = 0.325$, $P = 0.569$). We regarded a brood as a first breeding attempt if it was initiated before

the laying date of the earliest known second brood at that study site and year by a ringed female that fledged at least one young from her first brood in that year. The second brood period started when a ringed individual laid the first egg after a successful first brood at a particular site and year. If a female had only one clutch in a season, and this was started during the first brood period, we considered it as a single-brooded female in that year. We defined a female as double-brooded if it had a brood in the second brood period, and also had at least one nestling hatched in an earlier brood in the same year. Females sometimes used the same nest boxes for both their first and second broods, whereas they sometimes laid the second clutch in a different nest box. We detected double-brooding in both cases because we regularly checked unoccupied nest boxes through the whole breeding season. There was a temporal overlap between the termination of the last nesting attempt (we estimated that nestlings fledged out at age 19–21 days) in the first brood period (i.e., when the nestlings fledge from the nest) and the start of the first nesting attempt in the second brood period (i.e., when the first egg was laid) in all study sites (mean ± SD overlap, Veszprém: 12.86 ± 12.12 days, Balatonfüred: 8 ± 11.26 days, Szentgál: 11.71 ± 5.7 days, Vilma-puszta: 4 ± 5.9 days). Finally, we excluded broods that were the first known annual breeding attempts of identified females during the second brood period, because these females might have had a first brood that we did not detect (e.g., in natural cavities or nest boxes in private gardens) thus we cannot reliably decide whether these were single- or double-brooded females (number of excluded broods, Veszprém: 23, Balatonfüred: 9, Szentgál: 40, and Vilma-puszta: 5). Our final sample size thus included 822 broods produced by 387 females (number of broods and females: Veszprém: 319/121, Balatonfüred: 134/70, Szentgál: 249/122, and Vilma-puszta: 120/74). Females could breed in >1 year, resulting in 585 female-year combinations (i.e., yearly breeding by the 387 females).

Statistical analysis

First, to analyze the difference in the probability of double-brooding between study sites, we used binomial generalized linear mixed-effects models with logit link function (package *lme4* in R 3.4.4, Bates et al. 2015). The response variable was the females' annual breeding status (coded binary as 0: single-brooded and 1: double-brooded), and the predictors were study site (4 levels), female's age (FY or AFY), and the success of the first annual brood of the female (successful or failed). The 4th predictor was laying date (calculated as the number of days elapsed from 1 January until the laying of the first egg for each brood, where Day 1 = 1 January) which was mean-centered separately for each site within each year (thus expressed the relative time of laying within a population in a particular year). We included the year and female ID as crossed random effects.

Second, to compare the probability of double-brooding between habitat types (urban vs. forest) we used a pre-planned comparison (Ruxton and Beauchamp 2008). To do this, we calculated an urban forest linear contrast from the marginal means estimated for each study site in the above-described model (using the "contrast" function of the *emmeans* package, Lenth et al. 2019). Thus, we treated the 4 sites statistically as if they were 2 treatment groups and 2 control groups in an experiment, and we used a pre-planned comparison to test the prediction of whether the 2 treatment (i.e.,

urban) groups differ from the 2 control (i.e., forest) groups. With this method, we could test urban forest habitat differences while controlling for the potentially confounding site effect without running into the statistical problems of having too few random factor levels, which would happen if the study site was included as a random factor in the model (Piepho et al. 2003; Bolker et al. 2009). Similarly, we used the same marginal means to conduct the following between-sites pairwise comparisons: Veszprém vs. Szentgál, Veszprém vs. Vilma-puszta, Balatonfüred vs. Szentgál, and Balatonfüred vs. Vilma-puszta (i.e., all urban vs. forest site pairwise comparisons). The *P*-values of these pairwise comparisons were adjusted using the false discovery rate (FDR) method.

Third, to analyze the number of fledglings produced annually by females (i.e., the number of chicks fledged from a female's first plus, if double-brooded, second broods) we used a generalized linear mixed-effects model with Poisson error distribution (package *lme4*). In this model, the response variable was the annual number of fledglings, and predictors were the female's annual breeding status (single- or double-brooded), study site (4 levels), the breeding status × study site interaction, the success of the first seasonal brood of the female (successful or failed), and mean-centered laying date. We initially also included female age as a further predictor, but we removed it from the model because it had no significant effect ($P = 0.818$), and removing it improved the model's fit (the model's AIC (Akaike information criterion) value decreased from 2861.9 to 2859.9). Female ID and year were included as crossed random factors. We used pre-planned comparisons of linear contrasts (as described above) to compare the annual number of chicks produced by females between urban and forest habitats. Besides, we conducted 4 more pre-planned pairwise comparisons between specific groups of females: (1) urban single-brooded females vs. forest single-brooded females and (2) urban double-brooded females vs. forest double-brooded females (to test the effect of habitat type within single- or double-brooded females, respectively), (3) urban double-brooded females vs. forest single-brooded females (to test whether double-brooded urban females can produce the same or higher number of nestlings than single-brooded forest females), and finally (4) we tested whether the differences in the number of fledglings between single- and double-brooded females differ between the 2 habitats.

Finally, to provide some background information on other components of reproductive success, we also analyzed in 2 separate models (1) the total number of eggs and (2) the total number of hatchlings produced annually by females (i.e., the number of eggs and hatchlings produced in a female's first plus, if double-brooded, second broods). The model structure used in these analyses was similar to that described above for the analyses of the annual number of nestlings. We present these results as Supplementary data (Supplementary Tables S4 and S5).

Results

Probability of double-brooding

During the study period, 44% of urban and 36% of forest females were double-brooded in at least 1 year. We found significant differences between the study sites in the probability of double-brooding (Figure 1 and Table 1). The pre-planned comparison between urban and forest habitats (i.e., the 2
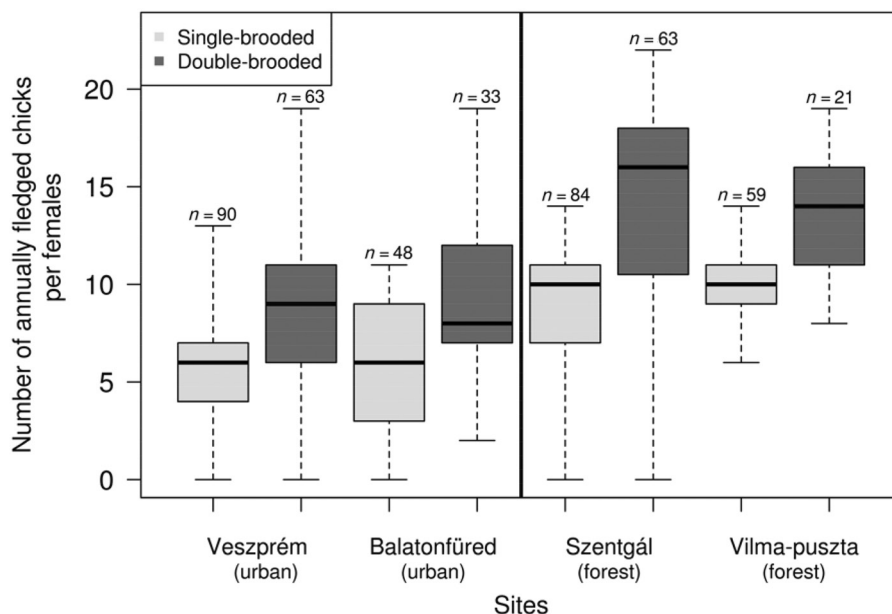
Figure 1. The proportion of double- vs. single-brooded female great tits at the 4 study sites (2013–2019; urban sites: Veszprém and Balatonfüred; forest sites: Szentgál and Vilma-puszta). Black dots and associated whiskers show mean and 95% confidence intervals as estimated from the binomial model (back-transformed from log odds ratio). Sample size (number of females) is presented below each box. Summary statistics for the model are presented in Supplementary Table S2.

Table 1. The effects of study site, female age, the success of the first seasonal brood, and laying date on the probability of double-brooding by female great tits

Predictors	χ^2	df	P-value
Intercept	0.299	1	0.585
Study site	10.670	3	**0.013**
Female age	3.966	1	**0.046**
Success of first seasonal brood	3.372	1	*0.066*
Mean-centered laying date	30.428	1	**< 0.001**

The table shows type 3 ANOVA (analysis of variance) results from the generalized linear mixed-effects model with binomial distribution (see Supplementary Table S2 for parameter estimates). Statistically significant ($P < 0.05$) differences are highlighted in bold and marginally nonsignificant ($0.05 < P < 0.1$) differences are highlighted in italics. $N = 822$ broods produced by 387 females.

urban vs. the 2 forest sites) indicated a marginally nonsignificant difference, with a trend for a higher probability of double-brooding in urban than forest birds (Table 2). The pre-planned pairwise comparisons between urban and forest study sites revealed a significantly lower probability of double-brooding in Vilma-puszta (forest) than in Veszprém (urban), whereas the difference between Vilma-puszta and the other urban site, Balatonfüred was marginally nonsignificant. The other forest site, Szentgál, did not differ from either of the 2 urban sites in the probability of double-brooding (Table 2 and Figure 1).

We also found that AFY females had a higher probability of double-brooding than FY females (Table 1). Double-brooded females laid their first eggs earlier than single-brooded females (Table 1), and there was a marginally non-significant trend for a higher probability of double-brooding in females with failed seasonally first breeding attempts (Table 1 and Supplementary Table S2).

Number of fledglings produced annually

We found that, as expected, double-brooded females produced more fledglings annually than single-brooded females (Table 3). The number of annually produced fledglings also differed between study sites, and there was a significant interaction between the effects of female breeding status (single- vs. double-brooded) and study site (Table 3 and Figure 2). The pre-planned comparison between habitats showed that urban females produced significantly fewer fledglings annually than their forest conspecifics (Table 4), and this habitat difference was also present both within single- and double-brooded females (Table 4). Furthermore, we found no significant difference in the number of fledglings between urban double-brooded and forest single-brooded females (Table 4), indicating that urban double-brooded females produced about the same number of fledglings annually as forest females from a single brood (Figure 2). The difference in the number of fledglings between single- and double-brooded females was significantly greater in forests than in urban habitats (Table 4).

Laying later in the season had a negative effect on the number of fledglings produced annually (Table 3 and Supplementary Table S3). Furthermore, females with failed first broods produced seasonally fewer fledglings than females with successful first breeding attempts (Table 3 and Supplementary Table S3).

Discussion

Probability of double-brooding

The lower reproductive success per breeding attempt in urban compared with rural bird populations is a well-documented phenomenon in many species (Chamberlain et al. 2009; Rodewald and Gehrt 2014; Sepp et al. 2017). In urban landscapes, several environmental factors could increase the propensity of double-brooding (see Introduction), which in turn may significantly increase urban birds' overall reproductive output and hence may reduce the actual habitat difference in breeding success. Yet, the vast majority

Table 2. Differences in the probability of double-brooding between (A) habitat types and (B) study sites (urban sites: Veszprém and Balatonfüred; Forest sites: Szentgál and Vilma-puszta)

Predictors	Comparisons	Contrast ± SE	Odds ratio ± SE	z ratio	Adjusted P-value
A)	Urban—Forest (habitat type)	0.426 ± 0.213	1.531 ± 0.327	1.995	*0.076*
B)	Veszprém—Szentgál (study sites)	0.021 ± 0.234	1.022 ± 0.239	0.092	0.927
	Veszprém—Vilma-puszta (study sites)	0.945 ± 0.305	2.572 ± 0.784	3.097	**0.009**
	Balatonfüred—Szentgál (study sites)	−0.093 ± 0.300	0.911 ± 0.273	−0.311	0.927
	Balatonfüred—Vilma-puszta (study sites)	0.830 ± 0.361	2.293 ± 0.827	2.302	*0.053*

The table shows the results of linear contrasts that were calculated from the binomial model presented in Table 1. P-values were adjusted for multiple testing using the FDR method, statistically significant ($P < 0.05$) differences are highlighted in bold, and marginally non-significant ($0.05 < P < 0.1$) differences are highlighted in italics. $N = 822$ broods produced by 387 females.
Contrasts are given as differences in log odds ratios. Odds ratio values are the exponentially back-transformed contrasts that provide the ratio of odds that a female being double-brooded in urban sites relative to forest sites. Thus an odds ratio >1 indicates an increased probability of double-brooding in the urban habitat (A) or urban study sites (B), whereas odds ratio <1 indicates an increased probability of double-brooding in the forest.
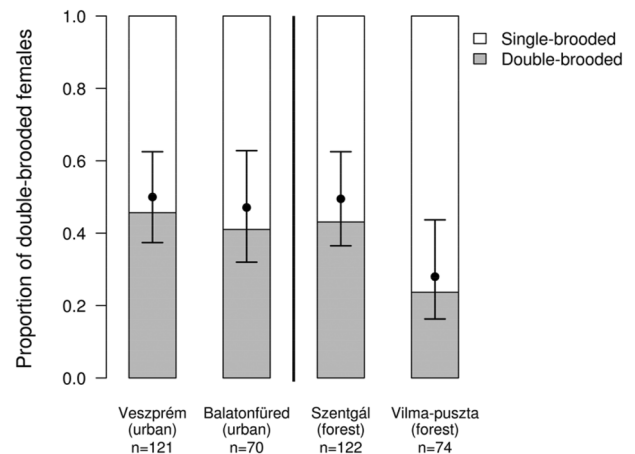
Table 3. The effects of female's annual breeding status (single- or double-brooded), study site, the breeding status× study site interaction, the success of the first seasonal brood, and the laying date on the annual number of fledglings produced by females

Predictors	χ^2	df	P-value
Intercept	17.846	1	< 0.001
Female's annual breeding status	86.532	1	< 0.001
Study site	149.287	3	< 0.001
Success of first seasonal brood	147.554	1	< 0.001
Mean-centered laying date	8.234	1	0.004
Female's annual breeding status × study site	10.692	3	0.013

The table shows the type 3 ANOVA results from the generalized linear mixed-effects model with Poisson distribution (see Supplementary Table S3 for parameter estimates). Statistically significant ($P < 0.05$) differences are highlighted in bold. $N = 822$ broods produced by 387 females.

Figure 2. Differences in the number of fledglings produced annually by single- and double-brooded females in the 4 study sites (data pooled from all years). Urban sites: Veszprém and Balatonfüred; forest sites: Szentgál and Vilma-puszta. On the box plots, medians and interquartile ranges are indicated by the thick middle lines and the boxes, respectively, while the whiskers extend to the most extreme data points within 1.5 × interquartile range from the box. Sample size (number of females) is presented above each box. Females that were single-brooded in 1 year and double-brooded in another year, are included in both categories of the study site.

of studies published so far—including those on great tits—focused on seasonally first broods without considering multiple breeding attempts per season. Therefore, we used our long-term dataset to conduct a comprehensive comparison of the frequency of double-brooding between habitats and assessed its consequences on the annual reproductive success of females.

Contrary to our expectations, we found that the probability of double-brooding was not consistently higher in urban than in forest populations. Several features of the urban environments may explain these results. First, previous studies showed that high-quality food is often limited in cities during the breeding season (Marciniak et al. 2007; Nadolski et al. 2021), resulting in increased rates of starvation-related mortality and detrimental impacts on nestling development and fledging success (Seress et al. 2018, 2020). The relative scarcity of natural food sources may also limit urban birds' multi-brooding propensity (Verboven et al. 2001; Batey 2018), either because females cannot find enough food to produce new clutches or because it is difficult and energetically expensive for the parents to provide enough prey items for their nestlings (Jarrett et al. 2020). The pre-fledging period could also be longer in urban habitats due to the slower development rate of nestlings (Corsini et al. 2020), which may eliminate the effect of seasonally earlier onset of breeding in cities. Additionally, if juvenile birds need increased or prolonged parental care during their post-fledging period, for example,

due to the difficulties of finding food sources independently, this could also decrease the probability of double-brooding for their parents (Verhulst and Hut 1996; Grüebler and Naef-Daenzer 2008). Finally, the propensity of double-brooding may also be at least partially a genetically determined trait, and the lack of sufficient genetic variation between populations may constrain changes in the tendency for double-brooding (Timm et al. 2019; Linder et al. 2021; Watson et al. 2021).

Collectively, our results and the few other studies highlight that urbanization has a highly variable effect on the frequency of double-brooding in urban bird populations. In great tits, Cowie and Hinsley (1987) found a higher number of second clutches in the city, whereas Luniak (1992) reported more second clutches in forests. In northern cardinals (*Cardinalis cardinalis*), there was no difference between urban and rural populations either in the number of the birds' annual nesting attempts or in their annual reproductive success (Leston and

Table 4. Differences between habitat types and female categories in the number of fledglings produced

Contrasts	Contrast ± *SE*	Ratio ± *SE*	z ratio	*P*-value
A) Urban—Forest, all females	−0.412 ± 0.031	0.663 ± 0.02	−13.242	**< 0.001**
B) Urban—Forest, single-brooded females	−0.475 ± 0.042	0.622 ± 0.026	−11.221	**< 0.001**
C) Urban—Forest, double-brooded females	−0.348 ± 0.045	0.706 ± 0.032	−7.683	**< 0.001**
D) Urban double-brooded females—Forest single-brooded females	< 0.0001 ± 0.041	1 ± 0.041	0.023	0.981
E) Urban single-brooded vs. double-brooded—Forest single-brooded vs double-brooded	−0.126 ± 0.061	0.811 ± 0.054	−2.042	**0.041**

The table shows the results of linear contrasts that were calculated from the model presented in Table 3. Statistically significant (*P* < 0.05) differences are highlighted in bold. *N* = 822 broods produced by 387 females.
Contrasts are given as differences between the compared groups (on the natural logarithm scale). The ratio shows the exponentially back-transformed contrast estimates that provide the ratio of the number of fledglings in urban sites compare to forest sites. Ratios >1 mean that the number of fledglings is higher at the urban habitat, whereas ratios <1 mean that the number of fledglings is higher in forest.

Rodewald 2006). Acadian flycatchers *Empidonax virescens* in urban sites attempted fewer clutches and had a lower annual reproductive success than in rural habitats, perhaps due to the greater incidence of brood parasitism in the cities (Rodewald and Shustack 2008). African crowned eagles *Stephanoaetus coronatus* breeding in more urbanized environments produced fewer fledglings per nesting attempt than birds breeding in less urbanized sites (similarly to the great tits in our study), but urban eagles had annually more nesting attempts which resulted in a similar annual reproductive success along the urbanization gradient (Muller et al. 2020). The reasons for the heterogeneity between these results may include differences in local habitat conditions (Smith et al. 2016) and also ecological and life-history differences between species.

In our study, habitat heterogeneity might have contributed to the difference we found between the 2 forest sites in the probability of double-brooding. For example, these 2 sites have different tree species compositions (see Materials and Methods section), which may influence the amount and seasonal distribution of phytophagous arthropods both during the egg-laying and the nestling development period. For example, caterpillar peak occurred 1 week later in Vilma-puszta than in Szentgál in 2 out of 4 years (see Table 1 in Seress et al. 2018). Furthermore, other cavity-nesting birds (e.g., blue tits *Cyanistes caeruleus*, collared flycatchers *Ficedula albicollis*, and Eurasian tree sparrows *Passer montanus*) frequently breed in the nest boxes in the forest sites, and the proportion of nest boxes occupied by these interspecific competitors may differ between the sites. Nest predation by fat dormice (*Glis glis*) and aesculapian snakes (*Zamenis longissimus*) is a common cause of brood loss in the forest populations and its frequency and seasonal dynamics could also differ between the sites. Interspecific competition and nest predation pressure can influence the frequency of double-brooding by affecting nest site availability, competition for food, and also the chance of rearing a second brood successfully. However, further studies are needed to understand the effects of these factors on the number of nesting attempts of great tits.

According to our results, those female great tits who start to breed earlier in the breeding season have a higher probability of double-brooding, which is in line with the findings of earlier studies conducted in other species (Bryant 1979; Monroe et al. 2008, but see Husby et al. 2009). Furthermore, older (i.e., AFY) females have a higher probability of

double-brooding than FY females, which is likely related to the higher familiarity of the older birds with the available food sources, nesting sites, and to their improved skills to compete for these resources (Hoffmann et al. 2015; Pigeault et al. 2020). The improved breeding performance with age may also be the consequence of the increase of reproductive effort with age, according to the residual reproductive value hypothesis (Williams 1966, but see Desprez et al. 2011). Moreover, failure of the first clutch affected positively the initiation of a second clutch, which is a common phenomenon and probably works as a compensation strategy for the loss of the first clutch (Tinbergen 1987; Mulvihill et al. 2009).

Number of fledglings produced annually

Our results clearly showed that the annual number of fledglings was much lower in cities than in the forests, and the difference was present both within single- and double-brooded females. This result is in line with the findings of the earlier studies which compared the success of annual first broods between urban and forest breeding great tit populations (Bańbura and Bańbura 2012; Wawrzyniak et al. 2015; de Satgé et al. 2019). In addition, our study showed that urban females need to produce 2 broods annually to have the same average number of offsprings as the forest females produce from a single brood.

We found that the later start of the first clutch within the breeding season has a negative effect on the number of annually fledged chicks, which is probably related to the decrease in food availability over the season (Batey 2018; Seress et al. 2018). Unsurprisingly, females whose first clutch in the breeding season failed had seasonally fewer fledglings than females whose first clutch was successful. We also found a breeding status × study sites interaction (Table 3 and contrast E in Table 4), meaning that having a second brood had a different effect on the number of fledglings in different sites/habitats. Specifically, this result indicates that females in the cities can produce fewer additional offspring by a second brood than forest females (see Figure 2, and the negative contrast in Table 4). This result can be explained by the generally lower number of nestlings per brood in the urban sites, both in the first and the second broods.

The consistently lower annual number of nestlings in urban populations could lead to lower fitness (Tinbergen and Sanz 2004; Carro et al. 2014) potentially resulting in a negative impact on population viability. Despite this, in some bird species including great tits population density is often similar or

sometimes even higher in cities than in more natural habitats (Møller et al. 2012, our unpublished data). This latter phenomenon implies that other mechanisms in cities may partly or completely compensate for the lower annual reproductive success. For example, the milder climate (Grimmond 2007) and the abundant human-provided food sources in cities could lead to better overwinter survival in urban compared with nonurban habitats (Robb et al. 2008; Evans et al. 2015; Sepp et al. 2017). Another possibility is that the high urban population densities are maintained by individuals dispersing from surrounding natural habitats into the cities. Unfortunately, the connectedness of urban and nonurban bird populations is poorly understood. The very limited evidence in tits, however, does not support a strong role of immigration in maintaining urban populations: for example, in a study conducted in Barcelona, migration appeared to be more prevalent from the city to the forest than vice versa (Björklund et al. 2010; Senar and Björklund 2021). In sum, the low annual reproductive output of individuals in some urban bird populations makes the self-sustaining of these populations questionable and warrants further studies (Narango et al. 2018).

Our study has some limitations. First, we estimated the annual reproductive output of the females from the number of fledglings, but there are other proxies which can estimate fitness more accurately (e.g., the number of recruits). Second, the estimates of the frequency of double-brooding and the annual number of fledglings are based on data of females that bred in nest boxes. Since females occasionally breed in other nest sites (e.g., in cavities in trees and buildings) in both habitat types, some nesting attempts can remain undetected influencing the estimates of the reproductive output. Consequently, for a better understanding of the dynamics of urban populations, further long-term studies are needed on key demographic parameters, including multiple-brooding, FY and adult survival, and migration between urban and nonurban habitats. Because the extent of urbanized areas is continuously increasing worldwide and urban areas hold significant populations of many bird species, such knowledge may help the future conservation of their populations.

Authors' Contributions

B.B. and A.L. conceived the study. B.B., G.S., and A.L. designed and B.B. conducted the statistical analyses. All authors collected the data. B.B., G.S., and A.L. wrote the first version of the manuscript with contributions from I.P., K.S., and E.V. B.B., G.S., and A.L. revised the manuscript with comments from I.P., K.S., and E.V.

Conflict of Interest Statement

The authors declared that they have no conflict of interest to this work.

Ethical Statement

All procedures applied during the research presented here were in accordance with the guidelines for animal care outlined by ASAB/ABS (www.asab.org) and Hungarian laws. We have all the required permissions for capturing and measuring birds and monitoring their breeding from the Balaton Upland National Park (permit number: 9135-2/2004, 2255/2008) and from the Government Office of Veszprém County, Nature Conservation Division (former Middle Transdanubian Inspectorate for Environmental Protection, and Natural Protection and Water Management; permit numbers: 31559/2011, 24861/2014, and VE-09Z/03454-8/2018).

Supplementary Material

"Supplementary material can be found at https://academic.oup.com/cz".

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