

# Comparison of nestling diet between first and second broods of great tits *Parus major* in urban and forest habitats

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## Abstract

*Comparison of nestling diet between first and second broods of great tits Parus major in urban and forest habitats.* To understand why early broods tend to be more successful than late broods we investigated the nestling diet and reproductive success of great tit pairs that had both a first and a second brood in the same breeding season. We found that in forest habitats great tit parents delivered similar composition and amount of food per nestlings throughout the breeding season, resulting in similar nestling body mass and survival in both first and second broods. In urban habitats, however, although parents provided similar amounts of food to the second broods they tended to deliver fewer caterpillars. In parallel with this, we observed lower nestling survival in second urban broods than in first broods even though the body mass of surviving nestlings was similar to that of the first broods. These findings suggest that although parents produce smaller second broods in both habitats, they are able to compensate for lower food availability in forest habitats but not in urban habitats, thus leading to reduced food quality and lower offspring survival in urban second broods.

**Key words:** Food availability, Nestling diet, Caterpillar, Urbanisation, Multiple brooding, Date hypothesis, Nestling food

## Resumen

*Comparación de la alimentación entre la primera y la segunda puestas de pollos de carbonero Parus major en hábitats urbanos y forestales.* Para comprender por qué las primeras puestas suelen tener más éxito que las últimas, estudiamos la alimentación de los pollos y el éxito reproductivo de las parejas de carboneros que tuvieron la primera y la segunda puestas en la misma temporada de cría. Observamos que en los hábitats forestales, los progenitores de carbonero podían aportar aproximadamente la misma cantidad de alimentos de composición similar por pollo durante toda la temporada de cría, lo que daba lugar a que la masa corporal y la supervivencia de los pollos de la primera y la segunda puestas fueran parecidas. Sin embargo, en los hábitats urbanos, los progenitores podían aportar una cantidad similar de alimentos, pero solían llevar menos orugas a los pollos de las segundas puestas. Asimismo, observamos que la supervivencia de los pollos de las segundas puestas era menor en hábitats urbanos, si bien la masa corporal de los pollos supervivientes era parecida a la de los pollos de las primeras puestas. Estos resultados sugieren que, aunque los progenitores producen segundas puestas más pequeñas en ambos hábitats, este mecanismo les permite compensar la menor disponibilidad de alimentos únicamente en los hábitats forestales, pero no en los urbanos, lo que conlleva que, en las segundas puestas en hábitats urbanos, la calidad de los alimentos sea peor y la supervivencia de la prole menor.

**Palabras clave:** Disponibilidad de alimentos, Alimentación de los pollos, Oruga, Urbanización, Puestas múltiples, Hipótesis de la fecha

## Introduction

Seasonal declines in reproductive performance have been observed in a wide variety of avian taxa (Price et al 1988, Perrins and McCleery 1989). For example, clutch size (Hochachka 1990, Mägi and Mänd 2004, Kaliński et al 2009, Winkler et al 2020), number of fledglings (Stodola et al 2009, Winkler et al 2020, Bukor et al 2021), fledging success (Mägi and Mänd, 2004; Öberg et al 2014), nestling mass/growth rate (Sedinger and Flint 1991, Jensen et al 2023), and recruitment (Hochachka 1990, Lambrechts et al 2008) often decrease with a later hatch date within the reproductive season. Two main hypotheses have been proposed to explain why early breeders are more successful than late breeders (Verhulst and Nilsson 2008). The parental quality hypothesis proposes that the seasonal decrease in reproductive success is caused by changes in the parents' phenotype. Individuals with higher phenotypic quality (for example, in better condition; Wendeln and Becker 1999) may reproduce at the start of the breeding season while lower quality pairs may reproduce later. This difference in parents' phenotype can result in a negative correlation between breeding time and breeding success. This idea has been supported, for example, by an experimental study by De Neve et al (2004) that compared the breeding success of first clutches (reared by foster parents) with induced replacement clutches of the same magpie *Pica pica* pairs. They found that breeding success of the pairs' replacement clutches was similar to that of their first clutches (reared by foster parents), and that some components of the breeding success of the replacement clutches were significantly higher than that for late-season first clutches of other magpie pairs. They concluded that within-individual variation cannot explain the seasonal variation, and therefore among-individual variation in parental quality is a more likely explanation for differences between early breeders and late breeders in magpies.

According to the date hypothesis, seasonal changes in the environment (such as food availability) are the primary cause of this negative trend. For example, many insectivorous birds, especially passerines, rely on caterpillars in their nestling rearing period (Krištín and Patočka 1997, Sinkovics et al 2021). The abundance of caterpillars, however, often shows strong seasonal patterns. In early spring caterpillar larvae are highly abundant (called 'caterpillar peak') while later in the season their biomass strongly decreases (Seress et al 2018, Laczi et al 2019, Smith and Smith 2019, Nadolski et al 2021). Several studies have highlighted the connection between caterpillar abundance and avian breeding success. Verboven et al (2001), for example, found that both clutch size and success of the first clutch were positively related to caterpillar density in individual territories, while Nagy and Holmes (2005) found that food availability was a strong predictor of double brooding of black-throated blue warblers *Setophaga caerulescens*. An experimental study on tree swallows *Tachycineta bicolor* found that nestlings in delayed hatching nests had poorer body condition and weighed less than their non-delayed counterparts,

and it was suggested this could be due to the lower biomass of available insects (Harriman et al 2017). As a consequence, according to the date hypothesis, nestlings hatched later in the season may develop in suboptimal food availability conditions, leading to their undernourishment and ultimately lower fledging success (Burger et al 2012, Kaliński et al 2019).

These two hypotheses are most likely non-mutually exclusive, and hatching date manipulation (that is, forcing females to lay a replacement clutch in order to delay their breeding time) is a frequently used method to experimentally investigate their relative importance (Verhulst et al 1995, Wardrop and Ydenberg 2003, De Neve et al 2004, García-Navas and Sanz 2011). Most of such experimental studies support both hypotheses even within the same study (Arnold et al 2004). For example, Verhulst et al (1995) concluded that 80-90% of the seasonal decline in reproductive success of great tits *Parus major* could be explained by environmental effects (i.e., by the date hypothesis), and the remaining 10-20% of decline would be due to differences in quality between the parents of early and late breeders. Moreover, some authors found temporal variation in the relative importance of the two processes. For example, Wardrop and Ydenberg (2003) found that in tree swallows the date hypothesis better explained the decline in nestling mass in the first half of the season, while the parent quality hypothesis better explained the second half.

In this study, our aim was to test predictions of the date hypothesis by analysing the nestling diet of the same great tit pairs that had both first and second broods within the same breeding season. Although this approach is less common, it could provide valuable information on the temporal changes in parental behaviour and/or nestling diet without further disturbing the nest, an inherent feature of nest manipulation experiments. The great tit is an ideal candidate species for this study because it often breeds twice a year in our study region and breeding success and nestling condition typically differ significantly between first and second broods (Dubiec and Cichoń 2001, Pimentel and Nilsson 2007, Bukor et al 2021). Caterpillars are the main component of great tits' nestling diet, and the chick-feeding behaviour of the parents is easy to monitor using cameras (Sinkovics et al 2018, 2021). We examined nestling diet in two habitats (at two forest study sites, and at two urban study sites) that differed markedly in food availability. In an earlier study, we found that the average caterpillar biomass during the birds' breeding season was 2-12 times higher (depending on the study year) in the forest than in the urban study sites (Seress et al 2018). Additionally, the forest habitats were characterized by a single large caterpillar biomass peak during the nestling rearing period of the first broods (around May), and this biomass decreased greatly until the breeding season ended. In the urban study sites, we also observed a seasonal decline in caterpillars in some, but not all, years and sites, and the decline was less pronounced because urban trees showed several small caterpillar peaks throughout the breeding season (see figure S3 in Seress et al 2018).

Because of this seasonal decline in food availability, we predicted changes in the amount and/or composition of the nestling diet and also a decrease in reproductive success. We selected 32 great tit pairs (10 forest, 22 urban pairs) that had two broods within the same breeding season and compared parental provisioning behaviour, nestling food composition, and breeding success between their annual first and second broods. Using video recordings of parental food deliveries, we determined the type and volume of individual food items brought to the nest. We predicted that the second broods in both habitats (1) would receive fewer caterpillars and higher proportions of other arthropods and/or non-arthropod (e.g., seeds) food items. We also predicted a lesser amount of nestling food in second broods than in first broods as the result of either (2) a lower feeding rate and/or (3) the delivery of smaller prey items. Due to the importance of large caterpillars for high fledging body mass and subsequent recruitment (Schwagmeyer and Mock 2008, Seress et al 2012, Sinkovics et al 2021), we also examined whether (4) the size of individual caterpillars delivered to the nest varied between first and second broods. Regarding breeding success, we predicted that second broods in both habitats would have lower (5) maximum brood size, (6) lower nestling body mass, and (7) lower nestling survival.

## Material and methods

### Study sites and field protocol

We collected data from three consecutive years (2014, 2015 and 2016) in two urban sites and two forest sites as part of a long-term monitoring scheme on the breeding biology of great tits in Hungary. Our urban study sites were in the cities of Balatonfüred (46° 57' 30" N, 17° 53' 34" E) and Veszprém (47° 05' 17" N, 17° 54' 29" E), where artificial nest boxes were placed in public parks, a cemetery, and university campuses where vegetation consists of both native and introduced species. The two forest sites were located in mature woodlands near Szentgál (47° 06' 39" N, 17° 41' 17" E; c. 3 km from the village of Szentgál, c. 20 km away from Veszprém) and Vilma-puszta (47° 05' 6.7" N, 17° 51' 51.4" E; c. 3 km from the edge of Veszprém). The Szentgál site is a beech *Fagus sylvatica* and hornbeam *Carpinus betulus* forest, whereas Vilma-puszta is dominated by downy oak *Quercus pubescens* and South European flowering ash *Fraxinus ornus*. At our study sites, great tits have stable nest-box breeding populations, and ca. one-third of the population initiated a second annual brood every study year (Bukor et al 2021). We checked the nest boxes at least every 3-4 days throughout each breeding season (from March to early July) to determine the breeding characteristics (laying date, clutch size, hatching date, and brood size). When the nestlings were 9-12 days old, we conducted standard video-recordings at the nests to collect data on the provisioning behaviour of parent birds (mean  $\pm$  SE, age of first vs. second broods, forest: 9.6  $\pm$  0.2 vs. 9.4  $\pm$  0.2 days, urban: 9.96  $\pm$  0.2 vs 9.79  $\pm$  0.2 days; hatching

day of the first nestling = day 1). We selected this age period because earlier studies have shown that the nestlings' food demand is highest around this age (Betts 1955, Van Balen 1973, Corsini et al 2021). Recording length was 60 minutes because this has shown to be suitable to characterize variation in parental provisioning in great tits (Pagani-Núñez and Senar 2013) and because among-pair differences are also detectable (Murphy et al 2015). Recordings started between 8:39 and 17:05 (mean  $\pm$  SE, first vs. second broods, forest: 13:12  $\pm$  00:40 vs. 11:44  $\pm$  00:29, urban: 12:20  $\pm$  00:30 vs. 11:46  $\pm$  00:27). At the start of each observation, we mounted a small camera (GoPro HD HERO 2 or 3) in a black plastic box outside the nest box (c. 15 cm from the entrance hole). These plastic boxes serve as camouflage for the cameras, and are constant accessories of our nest boxes; the breeding birds are familiar with them. Our earlier study showed that the presence of the cameras in the plastic boxes does not have detectable effects on the parents' behaviour (Seress et al 2017). A wooden shelf below the entrance hole was also attached to the nest boxes as parent birds often pause for a moment before entering the nest box. To avoid disturbing the parents' behaviour, the observers who mounted the cameras stayed away from the nest during the recording periods. The number of nestlings was counted before the start of each recording. We ringed and weighed nestlings (with a Pesola; precision of 0.1 g) when they were 14-17 days old (mean  $\pm$  SE, first vs. second broods, forest: 15.2  $\pm$  0.3 vs. 15.4  $\pm$  0.3; urban: 15.2  $\pm$  0.2 vs. 14.9  $\pm$  0.2; hatching day of the first chick = day 1). In order to identify the parents we captured them with a nest trap (see further details in Seress et al 2017) and individually marked them using one metal ring and three coloured plastic rings. The ringings and measurements were performed after the video observations because these events can influence parental behaviour (Seress et al 2017). Parent birds that were colour-ringed in earlier years (47 birds out of 64) or captured and marked during their first brood of a given breeding season were not re-captured.

### Video analysis and the studied variables

From the 60-min video recordings, we analysed the provisioning behaviour of individually identified pairs (i.e., both parents had coloured-rings) who had successfully raised both their first and second broods during a breeding season (with a minimum of one young fledged in each brood). Median hatching date and range of the observed nests are shown in table 1s. We procured observations for both brood types (i.e., first and second) for 32 pairs (10 forest and 22 urban), resulting in a total of 64 video samples (we have no forest nests from 2015, table 1s). We visually scanned these recordings using a VLC Media player (v. 2.2.0.; Free Software Foundation 1991). This software allows slow-motion and frame-by-frame playback. From the videos, we collected four variables to estimate the composition and amount of food provided to nestlings (summarised in table 1A) using methods we developed in earlier studies (Sinkovics et al 2018, 2021), as follows.

**Table 1.** The studied variables used to describe nestling diet and breeding success in the first and second broods of great tits. The table also shows the explanatory variables and random effects included in the initial models (i.e., step 1 in statistical analyses, see Methods for details). Two of the studied variables (non-caterpillar fraction of nestling diet and nestling survival) were analysed with Fisher's exact test/paired t-test (see text for justifications). Food data were collected from 60-min video recordings: \* Volume was calculated for all prey items using the same formula given for caterpillar volume

**Tabla 1.** Variables estudiadas utilizadas para describir la alimentación de los pollos y el éxito reproductor de los carboneros en la primera y la segunda puestas. En la tabla también se muestran las variables explicativas y los efectos aleatorios incluidos en los modelos iniciales (esto es, el primer paso de los análisis estadísticos; véase el apartado Methods para obtener información más detallada al respecto). Dos de las variables estudiadas (la proporción de la alimentación de los pollos no compuesta por orugas y la supervivencia de los pollos) se analizaron con la prueba exacta de Fisher y la prueba t pareada (consúltese el texto para ver las justificaciones). Los datos sobre alimentación se obtuvieron a partir de grabaciones de vídeo de 60 minutos: \* El volumen se calculó para todas las presas utilizando la misma fórmula dada para el volumen de las orugas.

Variable	Categories/calculation	Statistical models	
		Explanatory variables	Random factors
<b>A. Nestling food variables</b>			
1. Prey type	Caterpillar, other arthropod, non-arthropod, unidentified	1a. Caterpillar vs. non caterpillar Study site, brood type, year, date of observation, time of the day	Pair ID, brood ID
		1b. Non-caterpillar fraction (Analysed with Fisher's exact test)	
2. Feeding rate	$\frac{\text{Number of feeding visits per 60 min}}{\text{Number of nestlings}}$	Study site, brood type, year, date of observation, time of the day	Pair ID
3. Average prey volume*	$\frac{\text{Sum of the volume of measured prey items}}{\text{Number of measured prey items}}$		Pair ID
4. Caterpillar volume	$\pi l (0.5 w)^2$ l, length; w, mean width		Pair ID, brood ID
<b>B. Reproductive success variables</b>			
5. Maximum brood size	Maximum number of eggs minus the number of unhatched/broken eggs	Study site, brood type, year	Pair ID
6. Nestlings' body mass		Study site, brood type, year, nestling age	Pair ID, brood ID
7. Nestling survival	$\frac{\text{Number of ringed nestlings}}{\text{Maximum brood size}}$	- (Analysed using paired t-test)	

From the video-recordings we categorised the prey items delivered for each feeding visit into three prey types: caterpillars, other arthropods (e.g., spiders, mosquitos), and non-arthropod food items (e.g., seeds). We recorded a total of 953 parental nest visits and we were able to classify 594 prey items into the three prey type categories (table 2). Prey items that were not clearly visible (for example if the parent bird entered the nest box too fast) were classified as 'unidentified', and were included only in a subset of analyses (detailed below). Additionally, on 92 occasions, parent birds entered the nest box so fast that we were unable to determine the presence or absence of a prey item. We considered these 'uncertain events' as feeding events with 'unidentified' prey items because visits without prey items were very rare. We recorded only 15 prey-free visits, which is 1.8 % of the total number of feeding visits. Nest-visits without prey items were excluded from all calculations.

First, we used this prey type categorization data to compare (1) the proportions of caterpillars, other arthropods and non-arthropod food items between broods (unidentified prey items excluded). Second, we calculated (2) the feeding rate for each brood as the number of feeding visits in 60 minutes (both parents combined; and including unidentified prey items and uncertain events) divided by the number of nestlings counted before the recording. Third, to determine the amount of nestling food, we calculated prey volume for each prey item following the method of Sinkovics et al (2018, 2021). Briefly, we took a screenshot from the video record for each visible prey item when a parent bird held it in front of the nest box entrance hole. Then we measured the length and average width of the prey with software Fiji (in mm; excluding wings and legs, Schindelin et al 2012). We used the vertical diameter of the entrance hole as a size reference. This diameter was 32 mm in all nest boxes and was clearly visible on each screenshot. Our earlier experiment showed that

this method provides accurate and highly repeatable measurements of prey size (Sinkovics et al 2018). From these length and average width measurements, we calculated the volume of prey assuming they had the shape of a cylinder (Slagsvold and Wiebe 2007, prey volume =  $\pi l (0.5 w)^2$  where  $l$  and  $w$  are the length and the average width of a prey item, respectively). Due to the position of the camera (sideways), we were able to measure 375 prey items accurately. However, in many of the remaining cases we were unable to measure the exact length and/or width of a prey item, because, for example, the parent bird did not stand in front of the entrance hole. In such cases, we could instead estimate an approximate size of the prey relative to the birds' beak length and height (for the detailed description of the method please see Sinkovics et al 2021, Supplementary methods). Using this extrapolation, we were able to estimate volume for an additional 224 prey items; resulting in prey size data for a total of 599 prey items, as shown in table 2 (uncertain events were excluded, but unidentified measured prey items were included). From these data regarding prey volume, we calculated (3) the average prey volume for each brood (i.e., the amount of food delivered per feeding event), as the average volume of the prey items whose volume we were able to estimate during the 60-min observation (table 1A). We also estimated (4) the volume of each individual caterpillar using the method described above (table 2; unidentified prey items and uncertain events excluded). Finally, we used three variables to measure the differences in breeding success between first and second broods separately in forest and urban habitats (table 1B). (5) Maximum brood size was estimated as the maximum number of potentially hatched nestlings in a brood (calculated as the maximum number of eggs observed in the nest minus unhatched and broken eggs; table 3s). We also recorded (6) nestlings' body mass at ringing age (day 14–17 post-hatch), and (7) nestling survival as the number of ringed nestlings divided by the maximum brood size. For the analyses of reproductive success and nestling diet we used the same 32 pairs.

### Statistical analyses

We conducted all statistical analyses in R 3.4.3. (R Core Team 2017) using the following packages: 'nlme' (Pinheiro et al, 2022), 'emmeans' (Lenth 2018), 'MASS' (Venables and Ripley 2002), 'car' (Fox and Weisberg 2011), and 'multcomp' (Hothorn et al 2008). In general, our data analysis consisted of two consecutive steps. In the first set of models (step 1), we compared the first and the second broods within study sites. In step 2, we ran additional post hoc analyses that combine information from the two urban and the two forest sites to respectively compare first and second broods within habitat types. For the latter purpose, we applied pre-planned pairwise comparisons and followed the approach suggested by Ruxton and Beauchamp (2008) as this method is a powerful approach to test a priori hypotheses. We used this two-step approach rather than including habitat type as a fixed effect and site as a random effect in the models because variance estimates of random effects with few levels (only four

**Table 2.** Sample sizes of identified prey types and measured prey items in first and second broods within urban and forest habitats. Food data were collected from 60-min video recordings.

**Table 2.** Tamaño muestral de los tipos de presa identificados y ejemplares de presa medidos en la primera y la segunda puestas en hábitats urbanos y forestales. Los datos sobre alimentación se obtuvieron a partir de grabaciones de video de 60 minutos.

	Forest		Urban	
	First	Second	First	Second
Prey type	206	113	408	226
Caterpillar	116	70	133	62
Other arthropod	13	12	45	71
Non-arthropod	1	1	60	10
Unidentified	46	22	116	68
Uncertain events	30	7	47	8
Prey-free visits	0	1	7	7
Measured prey items	108	79	259	153
Caterpillar	88	65	106	57
Other arthropod	13	10	40	66
Non-arthropod	1	1	59	10
Unidentified	6	3	54	20

in our case) are unreliable (Bolker et al 2009, Vincze et al 2019). Furthermore, including both habitat type and site as fixed effects in the same model would lead to multicollinearity that would make our model estimates unreliable (Dormann et al 2013). Note that two variables (composition of the non-caterpillar fraction of the nestling food and nestling survival; table 1) were examined using Fisher's exact test and paired t-test, respectively, rather than mixed-effects models (see details in the respective sections below).

### Within-site comparisons between first and second broods (step 1)

In the first step, for each specific response variable (see table 1), we fitted a statistical model (see below) that included study site (four sites) and brood type (first/second) as predictor variables, and also their two-way interaction. In addition, each model contained the following potentially confounding variables: in the models testing the amount and composition of nestling food we added year, date of observation, and time of the day; in the analyses of maximum brood size we added only year; in the model of nestlings' body mass we added year and nestling age (table 1). Year was included in the models as a three-level factor (2014, 2015, 2016). Because the onset of the first and second broods varied between sites and years, we mean-centered the date of observation separately for each site, year, and brood type (first, second) combination in order to express the relative dates of video recordings for each population. To do this, we determined the hatching date of the first nestling for each site and year combination, separately for the first and second broods, and all observation dates were calculated

relative to these dates. This transformation reduced the multicollinearity of the date variable with year, site, and brood type in the models ( $VIF_{max} < 1.8$  in all cases). The time of the day variable was categorized as a three-level factor: between 8–11 h ( $n = 21$  records), 11–13 h ( $n = 18$  records), 14–17:05 h ( $n = 25$  records). Nestling age was a four-level factor (14, 15, 16, and 17 days old). We removed these additional confounding variables stepwise (by looking at the  $p$ -values in a type 3 ANOVA table generated from the initial and reduced models) until only statistically significant ( $p < 0.05$ ) confounding variables and the main predictor variables (site, brood type, site  $\times$  brood type) remained in the model. Because each pair has data from two broods in the analyses, we used pair ID as a random factor in all models. No pairs were included in these analyses from more than one breeding season. For each model, we checked the statistical assumptions of the models by examining the residual plots (Zuur et al 2009). We describe the details specific to each model below (because the predictor variables and model selection methods are common in each model, as described above, these are not repeated).

We examined seasonal differences in two aspects of food composition (i.e., prey types). First, to investigate the (1) proportion of caterpillars in nestling food (table 1A), we built a generalized linear mixed model (GLMM) with binomial error distribution and 'logit' link. Here, we used a binary response variable for prey type coded as caterpillars = 1, and all other identified food items = 0 (594 prey items; table 2). In this model, we added brood ID nested in pair ID as a random factor to control for repeated feeding events by the same pair. The difference between these two random factors is that the brood ID groups the feeding events belonging to one 60-minute observation, whereas pair ID connects the recordings of a pair's first and second broods. Second, we investigated the composition of the non-caterpillar fraction of the nestling food. However, since almost all non-caterpillar food items were classed as 'other arthropods' in the forest (we observed 'other' prey items only in two feeding events), we ran this analysis only in the urban habitat. Because the sample size was very low for some prey types even in the urban habitat (table 2), we used Fisher's exact test (instead of a linear model) to compare the ratio of non-caterpillar arthropod and non-arthropod food items between first and second urban broods (urban sites combined here). Only identified prey items were included in both food composition analyses (594 prey items in total; table 2).

Next, we conducted three analyses to investigate how the amount of nestling food varies between first and second broods (table 1A). We built separate linear mixed-effect model (LME) with the following response variables: (2) feeding rate, (3) average prey volume, and (4) caterpillar volume. In the models of feeding rate and average prey volume, we included pair ID as random factor, whereas in the caterpillar volume model we added brood ID nested in pair ID as random factor due to multiple data per brood. Caterpillar volume data were cube root transformed to meet the statistical assumptions of the models (Zuur et al 2009).

To investigate breeding success, we built separate linear mixed-effect models (LME) for (5) maximum brood size and (6) nestlings' body mass as response variables (table 1B). In the model of maximum brood size, we included pair ID as random factor, whereas in the nestlings' body mass model we added brood ID nested in pair ID as random factor. To analyse (7) nestling survival we used paired  $t$ -test, where we compared the average difference in nestling survival of first and second broods of each pair separately for forest and urban habitats (data of the sites within a habitat are combined here).

### Within-habitat comparisons between first and second broods (step 2)

In the second step of the analyses, we applied pre-planned pairwise comparisons to test the predictions separately for urban and forest habitats. To do this, we calculated marginal means of the response variables from the 'final' (after selection) models for first and second broods of each of our study sites using 'emmeans' package (Lenth 2018). Then, we calculated linear contrasts between first and second broods separately for urban and forest habitats (i.e., urban and forest study sites combined, respectively) from these marginal means derived from the models, and we used function 'glht' (in package 'multcomp') to test whether these contrasts (i.e., the difference between first and second broods) differed from zero within each habitat type. We applied the false discovery rate (FDR) method to correct  $p$ -values for multiple comparisons. In all analyses, we refer to  $0.05 < p < 0.1$  as a marginally non-significant trend effect.

## Results

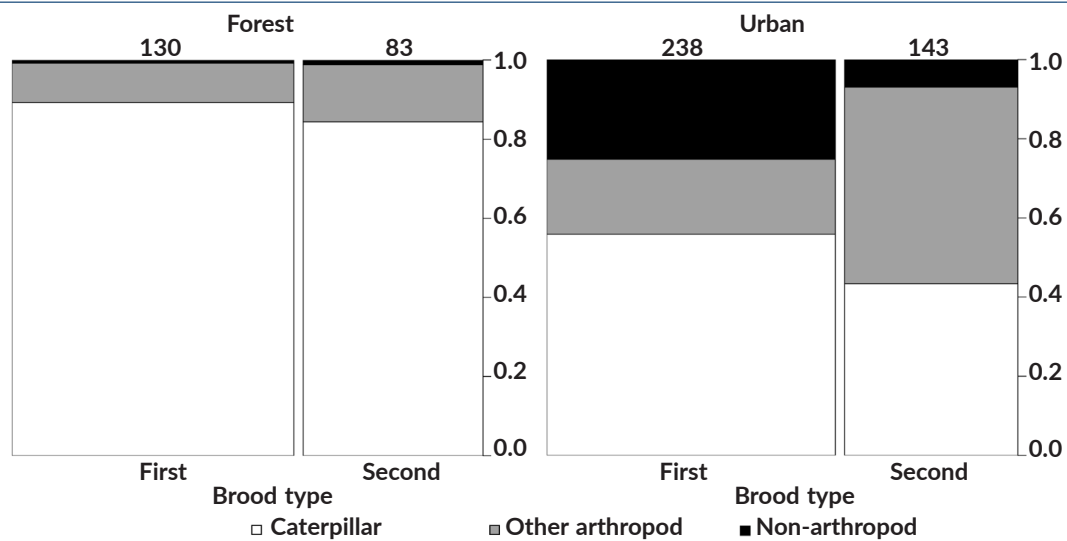
### Food composition

The statistical model for the (1) proportion of caterpillars in the nestling diet showed that the effect of the site  $\times$  brood type interaction was not significant (table 3A). The within-habitat linear contrasts indicated that forest great tit nestlings received a similar proportion of caterpillars in the first and second broods (89.2% vs. 84.3%; table 3B, fig. 1). However, in the urban habitat, nestlings reared in second broods tended to receive a smaller proportion of caterpillars than those in the first broods, although this difference was marginally non-significant (first vs. second broods: 55.9 vs. 43.4%; table 3B, fig. 1).

We found a significant association between brood types and the types of the non-caterpillar fraction (i.e., non-caterpillar arthropods versus non-arthropods) of nestling diet in the urban habitat (Fisher's exact test,  $p < 0.001$ ). Here, nestlings in second broods received higher proportions of other arthropods than other prey items compared to first broods (fig. 1). Other (i.e., non-arthropod) prey items were negligible in the diet of forest broods (fig. 1).

### Amount of nestling food

Regarding (2) feeding rate, we found that site  $\times$  brood type interaction was not significant (table 3A). Linear contrasts calculated from this model did not indicate



**Fig. 1.** Proportions of prey types (caterpillar, other arthropod, and non-arthropod) that forest and urban great tit nestlings received in first and second broods. Sample sizes of identified prey items are shown above the columns and within a panel are proportional to the width of the columns.

**Fig. 1.** Proporciones de diferentes tipos de presa (orugas, otros artrópodos y no artrópodos) que los pollos de carbonero de hábitats forestales y urbanos recibieron en la primera y la segunda puestas. El tamaño muestral de las presas identificadas que se muestra encima de las columnas y en un recuadro es proporcional al ancho de las columnas.

any significant difference in the feeding rate between first and second broods either in the forest or in the urban habitats (table 3B, fig. 2A). Similarly, in the comparison of the (3) average prey volume, the site  $\times$  brood type interaction was not significant (table 3A), and linear contrasts between first and second broods also showed no significant differences either in the forest or in the urban habitats. This observation indicates that in both habitats the size of the prey items per feeding visit was similar between first and second broods (table 3B, fig. 2B). For (4) caterpillar volume, we also found that site  $\times$  brood type interaction was not significant (table 3A) and linear contrast showed that the volume of caterpillars did not differ between first and second broods either in the forest or in the urban habitats (table 3B, fig. 2C). Year had a statistically significant effect in the feeding rate and average prey volume models, but not in the caterpillar volume model.

#### Breeding success

For (5) maximum brood size, we found that site  $\times$  brood type interaction was not significant (table 4A). Linear contrasts calculated from this model indicated that both in urban and forest habitat, maximum brood size decreased seasonally, meaning that parents in second broods reared fewer nestlings than in first broods regardless of habitat type (table 4B, fig. 3A). When comparing (6) nestlings' body mass, we also found that site  $\times$  brood type interaction was not significant (table 4A). Linear contrasts between first and second broods showed no significant differences either in the forest or in the urban habitats, meaning that nestlings' body mass at ringing age did not differ

between first and second broods (table 4B, fig. 3B). (7) In the urban habitat we observed a significant difference in nestling survival between first and second broods (average difference in nestling survival between first vs. second broods: 0.201;  $t = 4.157$ ;  $df = 21$ ;  $p < 0.001$ ,  $n = 22$  broods; fig. 3C). In contrast, we did not detect significant differences between first and second broods in the proportion of nestlings that survived from hatching to ringing in the forest habitat (average difference in nestling survival between first vs. second broods: 0.007;  $t = 0.23$ ;  $df = 9$ ;  $p = 0.823$ ,  $n = 10$  broods; fig. 3C). The year had a statistically significant effect on the nestlings' body mass but not on maximum brood size.

#### Discussion

In this study we explored the differences in nestling diet and reproductive success between first and second broods of the same breeding pairs in two habitat types that differed regarding the availability of caterpillars (the main component of nestling diet) during the breeding season. This design allowed us to study the potential effects of seasonal changes in food availability on reproductive success without the confounding effects of seasonally changing parental quality caused by the delayed breeding of low-quality pairs. Studies of second broods often examine the effects of a treatment on parental behaviour, observations without manipulation are relatively rare. Additionally, to the best of our knowledge, our study is the first to compare both the composition and the quantity of nestling diet between first and second broods in urban environments.

**Table 3.** Comparison of the composition and amount of nestling food between first and second broods in forest and urban habitats. Results of GLM/LM models (A) and the derived linear contrasts (B) (first broods compared to second broods in each habitat type) in the proportion of caterpillars in nestling food, feeding rate (number/nestling/hour), average prey volume (mm<sup>3</sup>/feeding visit), and caterpillar volume (mm<sup>3</sup>/specimen). Statistically significant ( $p < 0.05$ ) differences are highlighted in bold, whereas marginally non-significant trend effects ( $0.05 < p < 0.1$ ) are in italics. For linear contrasts, positive estimates indicate higher values in first broods. P-values were adjusted using the false discovery rate (FDR) method. Note that the rows are for different information in parts (A) and (B). Sample sizes (first vs. second broods): prey type (forest, 130 vs. 83; urban, 238 vs. 143 identified prey items); feeding rate, average prey volume (forest: 10 vs. 10 broods; urban: 22 vs. 22 broods); caterpillar volume (forest: 88 vs. 65; urban: 106 vs. 57 caterpillar specimens).

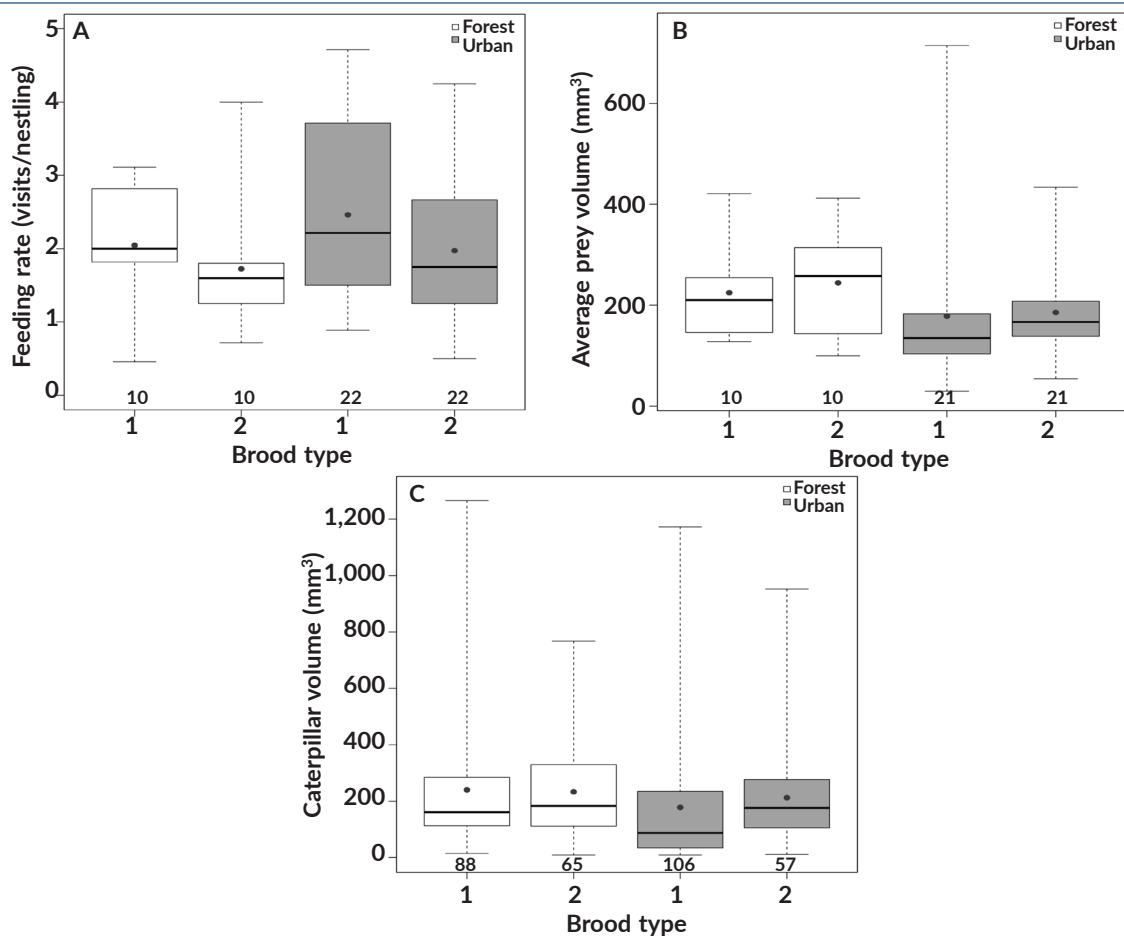
**Table 3.** Comparación de la composición y la cantidad de los alimentos que recibían los pollos entre la primera y la segunda puestas en hábitats forestales y urbanos. Resultados del modelo mixto lineal generalizado y el modelo lineal de efectos mixtos (A) y los contrastes lineales derivados (B) (se comparan las primeras puestas con las segundas en cada tipo de hábitat) en la proporción de orugas en la alimentación de los pollos, la tasa de alimentación (número/pollo/hora), el volumen medio de las presas (mm<sup>3</sup>/visita de alimentación) y volumen de las orugas (mm<sup>3</sup>/ejemplar). Las diferencias estadísticamente significativas ( $p < 0,05$ ) se destacan en negrita, mientras que los efectos de tendencia marginalmente no significativos ( $0,05 < p < 0,1$ ) se indican en cursiva. En el caso de los contrastes lineales, las estimaciones positivas indican valores más altos en las primeras puestas. Los valores de p se ajustaron utilizando el método de la tasa de descubrimiento falso. Obsérvese que las hileras contienen información diferente en las partes (A) y (B). Tamaño muestral (primera y segunda puestas): tipo de presa (forestal: 130 y 83; urbano: 238 y 143 presas identificadas); tasa de alimentación, volumen medio de las presas (forestal: 10 y 10 pollos; urbano: 22 y 22 pollos); volumen de las orugas (forestal: 88 y 65; urbano: 106 y 57 orugas).

A. GLMM/LME models				B. Linear contrasts between first and second broods in forest and urban habitats			
Predictors	df	$\chi^2$	p-value	Habitat	Contrast $\pm$ SE	t	Adjusted p-value
1. Caterpillar vs. non-caterpillar (GLMM)							
Site	3	32.165	< 0.001	Forest	0.723 $\pm$ 0.694	-	0.306
Brood type	1	3.555	0.059	Urban	0.772 $\pm$ 0.335	-	0.057
Site $\times$ brood type	3	1.112	0.774				
Random effects:		<b>SD</b>					
Pair		0.000					
Brood nested in pair		0.505					
Residual variance		0.958					
2. Feeding rate (LME)							
Site	3	1.476	0.688	Forest	0.209 $\pm$ 0.474	0.441	0.663
Brood type	1	1.228	0.268	Urban	0.526 $\pm$ 0.305	1.724	0.191
Year	2	6.887	<b>0.032</b>				
Site $\times$ brood type	3	0.338	0.953				
Random effect:		<b>SD</b>					
Pair		0.516					
Residual variance		0.848					
3. Average prey volume (mm <sup>3</sup> ; LME)							
Site	3	1.765	0.623	Forest	-23.840 $\pm$ 67.100	-0.355	0.895
Brood type	1	0.184	0.668	Urban	6.059 $\pm$ 45.418	0.133	0.895
Year	2	9.491	<b>0.009</b>				
Site $\times$ brood type	3	0.425	0.935				
Random effect:		<b>SD</b>					
Pair		0.012					
Residual variance		120.032					
4. Caterpillar volume (mm <sup>3</sup> ; LME)							
Site	3	6.657	0.084	Forest	-0.153 $\pm$ 0.527	-0.290	0.775
Brood type	1	1.782	0.182	Urban	-0.605 $\pm$ 0.431	-1.404	0.347
Site $\times$ brood type	3	1.961	0.581				
Random effects:		<b>SD</b>					
Pair		0.000					
Brood nested in pair		0.697					
Residual variance		1.533					

Regarding the (1) composition of nestling food, we found that in forest habitats nestlings both in first and second broods received high proportions of caterpillars (> 80%) and their diet did not differ significantly between the two brood types. In contrast, urban nestlings

in second broods tended to receive lower proportions of caterpillars and higher proportions of other arthropod food items (e.g., spiders) than first broods. However, the amount of nestling food [(2) feeding rate, (3) average prey volume, (4) caterpillar volume] did not differ





**Fig. 2.** The amount of food delivered to great tit nestlings during 60-min video observations in first and second broods in forest and urban habitats: A, feeding rate of parents (number/nestling/hour); B, average prey volume delivered by the parents to nestlings ( $\text{mm}^3/\text{feeding visit}$ ); C, the volume of caterpillar specimens delivered to great tit nestlings ( $\text{mm}^3$ ). Boxplots show the median (thick lines), mean (black dots) and the interquartile range, with the whiskers representing the range of data distribution. Sample sizes (number of broods for feeding rate and average prey volume, number of specimens for caterpillar volume) for each group are provided below the boxes.

**Fig. 2.** Cantidad de alimento entregada a los pollos de carbonero durante los 60 minutos de grabación en video en la primera y la segunda puestas en hábitats forestales y urbanos: A, tasa de alimentación de los progenitores (número/pollo/hora); B, volumen medio de las presas entregadas por los progenitores a los pollos ( $\text{mm}^3/\text{visita de alimentación}$ ); C, volumen de los ejemplares de oruga entregados a los pollos de carbonero ( $\text{mm}^3$ ). En los diagramas de caja se muestran la mediana (líneas gruesas), la media (puntos negros) y la amplitud intercuartílica; los bigotes representan el rango de distribución de los datos. El tamaño muestral (número de pollos para la tasa de alimentación y el volumen medio de las presas, número de ejemplares para el volumen de las orugas) de cada grupo se indica debajo de las cajas.

between first and second broods in either habitat. Regarding breeding success, parents in both habitat types reared (5) fewer nestlings in second broods. However, (6) nestlings' body mass did not differ between first and second broods. In the forest habitat, almost every hatched (7) nestling survived in both first and second broods. In contrast, urban nestlings in second broods had ca. 20% lower survival than first broods. We discuss these results in detail separately for each habitat type. Please note, however, that due to the low number of sampled pairs (especially in the forest habitat) some of the results should be treated with caution.

In forests, neither the composition nor the amount of food per nestling differed significantly between first and second broods. These results imply that even though caterpillar biomass decreased as the season progressed

(Seress et al 2018), great tit parents were able to deliver an approximately similar composition and amount of food to their nestlings. This may be feasible due to the lower brood size in second broods, a strategy that may be a response to the reduced food availability later in the season. As a result of fewer nestlings yet similar nestling diet, forest nestlings reached a high body mass and survival similar to that high in first broods. Although the relationship between the phenology of caterpillar abundance and breeding success has been observed in long-term studies including a forest tit species -the green-backed tit *Parus monticolus* (-), complex analyses of nestling diet (both the composition and amount) are rare, thus making comparison of results between studies difficult. Studies that examine the temporal changes of feeding rate without prey size, for example, may

**Table 4.** Comparison of breeding success between first and second broods in forest and urban habitats. Results of LME models (A) and the derived linear contrasts (B) (first broods compared to second broods for each habitat type) in maximum brood size and nestlings' body mass (g). Statistically significant ( $p < 0.05$ ) differences are highlighted in bold, whereas marginally non-significant trend effects ( $0.05 < p < 0.1$ ) are in italics. For linear contrasts, positive estimates indicate higher values in first broods. P-values were adjusted using the false discovery rate (FDR) method. Note that the rows are for different information in parts (A) and (B). Sample sizes (first vs. second broods): maximum brood size (forest: 10 vs. 10 broods; urban: 22 vs. 22 broods); nestlings' body mass (forest: 101 vs. 70; urban: 165 vs. 97 nestlings).

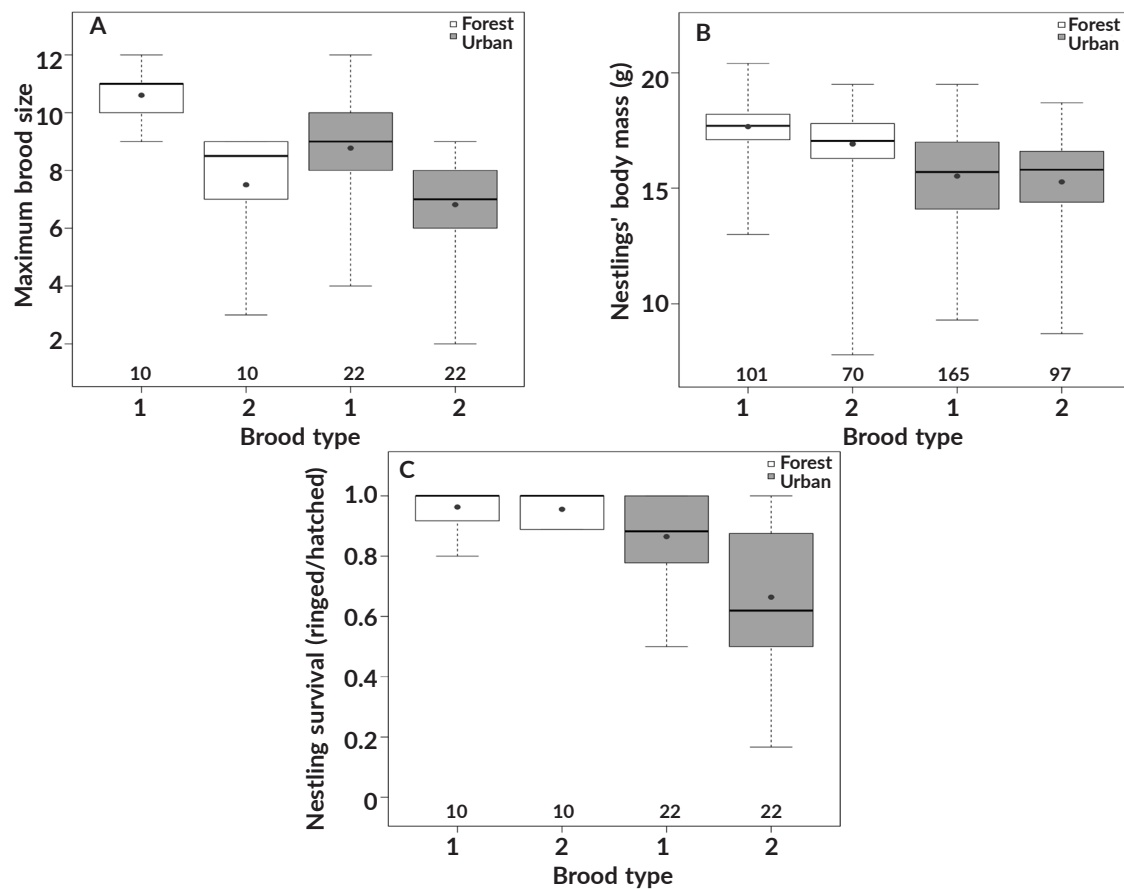
**Tabla 4.** Comparación del éxito reproductivo entre la primera y la segunda puestas en hábitats forestales y urbanos. Resultados de los modelos lineales de efectos mixtos (A) y los contrastes lineales derivados (B) (se comparan las primeras puestas con las segundas en cada tipo de hábitat) en el tamaño máximo de la puesta y la masa corporal (g) de los pollos. Las diferencias estadísticamente significativas ( $p < 0,05$ ) se destacan en negrita, mientras que los efectos de tendencia marginalmente no significativos ( $0,05 < p < 0,1$ ) se indican en cursiva. En el caso de los contrastes lineales, las estimaciones positivas indican valores más altos en las primeras puestas. Los valores de p se ajustaron utilizando el método de la tasa de descubrimiento falso. Obsérvese que las hileras contienen información diferente en las partes (A) y (B). Tamaño muestral (primera y segunda puestas): tamaño máximo de la puesta (forestal: 10 y 10 puestas; urbano: 22 y 22 puestas); masa corporal de los pollos (forestal: 101 y 70; urbano: 165 y 97 pollos).

Predictors	A. LME models			B. Linear contrasts between first and second broods in forest and urban habitats			
	df	$\chi^2$	p-value	Habitat	Contrast $\pm$ SE	t	Adjusted p-value
5. Maximum brood size							
Site	3	7.641	0.054	Forest	2.88 $\pm$ 0.719	4	< 0.001
Brood type	1	7.32	<b>0.007</b>	Urban	2.04 $\pm$ 0.463	4.413	< 0.001
Site $\times$ brood type	3	3.119	0.374				
Random effect:		<b>SD</b>					
Pair		1.233					
Residual variance		1.286					
6. Nestlings' body mass (g)							
Site	3	16.218	<b>0.001</b>	Forest	1.053 $\pm$ 0.659	1.599	0.242
Brood type	1	1.373	0.241	Urban	-0.157 $\pm$ 0.447	-0.352	0.728
Year	2	9.444	<b>0.009</b>				
Site $\times$ brood type	3	4.236	0.237				
Random effects:		<b>SD</b>					
Pair		0.357					
Brood nested in pair		1.084					
Residual variance		1.388					

have inconsistent results because parental provisioning activity can vary with prey size (Senécal et al 2021). Furthermore, some studies found a seasonal decline in feeding rate (Schwagmeyer and Mock 2003, Barba et al 2009) while others found no seasonal patterns (Bortolotti et al 2011). Regarding food composition, in an orange grove, Barba and Gil-Delgado (1990) and Barba et al (2004) found that the proportion of caterpillars in the nestling diet of great tits decreased over the season and adult moths became the most frequently provided food for the nestlings. The authors considered that the short period of caterpillar peak forced the birds to change and adapt prey type to seasonal availability and abundance. Another study from an evergreen forest in Corsica also observed that the proportion of caterpillars in blue tit nestlings' diet decreased later in the season, again suggesting a marked limitation of this prey in the area as the season progressed (Bañbura et al 1994). However, Lambrechts et al (2008) found different patterns in different types of forests. They reported a seasonal decrease in frass fall (a proxy of caterpillar biomass), clutch size, and the number of fledged young in a downy oak *Quercus humilis* forest

patch, and a seasonal increase of these characteristics in a holm oak *Quercus ilex* forest patch. Conversely, it seems that great tits in the forest population in our study were able to find enough caterpillars for their nestlings even later in the season to successfully rear the late-born nestlings mostly on that prey type, without needing to switch to other less optimal food types. Note, however, that beside caterpillars, other arthropods may also be important components of the nestling diet (e.g., spiders, Pagani-Núñez et al 2011).

In the urban habitat, we found that parents tended to provide fewer caterpillars to nestlings in second broods, and also that nestling survival was lower in second broods than in first broods. Although urban areas showed smaller caterpillar peaks and less pronounced caterpillar biomass decline throughout the breeding seasons of 2013-2016 (i.e., a period overlapping with that of the current study; see fig. 2 in Seress et al 2018) in our study the proportion of caterpillars in nestling diet decreased for second broods. Similarly, to the forest pairs, urban great tits also reduced their brood size in second broods, possibly as a response to declining food availability, and therefore, they were able to



**Fig. 3.** Breeding success of the 32 video-recorded great tit pairs in first and second broods in forest and urban habitats: A, maximum brood size (number of potentially hatched nestlings); B, nestlings' body mass (in g); C, nestling survival (number of ringed nestlings/maximum brood size). Boxplots show the median (thick lines), mean (black dots) and the interquartile range, with the whiskers representing the range of data distribution. Sample sizes (number of broods for maximum brood size and nestling survival, number of nestlings for nestlings' body mass) for each group are provided below the boxes.

**Fig. 3.** Éxito reproductivo de las 32 parejas de carbonero grabadas en video en la primera y la segunda puestas en hábitats forestales y urbanos: A, tamaño máximo de la puesta (número de huevos que podrían haber eclosionado); B, masa corporal de los pollos (en g); C, supervivencia de los pollos (número de pollos anillados/tamaño máximo de la puesta). En los diagramas de caja se muestran la mediana (líneas gruesas), la media (puntos negros) y la amplitud intercuartílica; los bigotes representan el rango de distribución de los datos. El tamaño de la muestra (número de pollos para el tamaño máximo de la puesta y la supervivencia de los pollos, número de pollos para la masa corporal de los pollos) de cada grupo se indica debajo de las cajas.

deliver similar amounts of food to their nestlings. In parallel with this, we found decreased nestling survival in first vs. second urban broods, possibly due to the lack of optimal food items, i.e., caterpillars. However, the surviving nestlings reached similar body mass in first and second seasonal broods. The combination of these results suggests that the adjustment of brood size to the local food supply is not optimal in our urban sites as, despite the smaller brood sizes, nestling survival was still lower in second broods. Although complex investigation of seasonal changes of nestling diet in urban habitats is rare, a study in Poland examined great tit nestlings' haemoglobin concentration in first and second broods in a parkland area that was characterized by highly fragmented tree cover and intense human disturbance (Kaliński et al 2009). The authors found food shortages for second broods in a year characterized by dry and hot weather (which was

not optimal for arthropod development). This resulted in lower haemoglobin levels but similar body mass of the nestlings compared to first broods. In contrast, in another year, the milder weather (moderately warm temperature with regular but not heavy rain) enabled the development of rich arthropod communities, and the haemoglobin concentrations in the blood of second brood nestlings were even higher and the birds were in a better condition than those in first broods. In a Portuguese suburban forest, Norte et al (2008) also found that nestlings from second broods had significantly lower haemoglobin levels and a tendency to a lower body condition index. They also hypothesized that these results could reflect malnutrition of the nestlings.

Our results, in summary, imply that our urban habitat might be similar to the above-mentioned 'poor' quality forest habitat, where great tits are forced to switch from

the preferred, optimal caterpillar prey items to other, less nutritious food types. A possible explanation for the difference we found in nestling food composition between first and second urban broods could be a difference in territory quality (i.e., second broods being in lower quality territories; Bañbura et al 1994). Indeed, in our study, 15 of the 22 urban great tit pairs (68.2%) moved to a different nestbox for their second brood. However, they mostly chose neighboring nestboxes (distance between the occupied nestboxes in first and second broods, mean  $\pm$  SE:  $43.6 \pm 4.4$  m). A recent study from Scotland found that chick-rearing blue tits in an urban parkland area flew c. 40 m for food on average (Jarrett et al 2020), and our own data also indicate that urban great tits mostly use a 60-m radius area around a nest (Seress et al in prep). Territories are thus probably overlapping considerably for first and second broods of the same urban pairs. Interestingly, in the forest, only 2 of the 10 forest parents (20%) changed nesting site for second broods in the same breeding season (distance between the two occupied nestboxes was 91 and 30 m for the two pairs, respectively), while the rest of eight parents stayed in the same nestbox (and territory) for both broods. It is therefore unlikely that differences in territory quality between first and second broods could have affected our results.

It is important to note that there may be other effects in the background that we did not assess in this study but that could also reduce nestling survival in the urban habitat. For example, our earlier study showed that the number of hot days can increase nestling mortality (Pipoly et al 2022) and as the season progresses, the frequency of hot days are likely to increase. However, in our study system, we found that the negative effects of hot weather on urban nestlings' body mass and survival were minor or less harmful to nestlings than in forests (Pipoly et al 2022). On the other hand, ectoparasites can also influence parental provisioning (Schoepf et al 2022) or reduce nestling body conditions (O'Brien and Dawson 2008), and high levels of parasite load can lead to nestling mortality. For example, an experimental study on house martins *Delichon urbica* in Badajoz city, Spain, showed that the ectoparasitic house martin bug *Oeciacus hirundinis* had higher negative effects on its host's reproduction during second clutches than in first clutches when environmental conditions for reproduction were deteriorated (de Lope et al 1993).

As we highlighted in the Introduction, the parental quality and date hypotheses are most likely non-mutually exclusive, and manipulation of breeding time without unwanted side effects seems to be impossible (reviewed in Verhulst and Nilsson 2008). Although our study does not allow for a clear separation of the two hypotheses, it does not seem that the reduced nestling survival for urban second broods is a consequence of parental feeding capacity (parental quality hypothesis), but is caused rather by the decrease of optimal food in nestling diet (date hypothesis). In our study, we aimed to control for parental quality by quantifying the feeding activity and breeding characteristics of the same parents within a breeding season. This observation method could also have disadvantages however. For example,

parental quality may not be constant over time. Some studies have reported weight loss in females during the breeding season and this, may affect parental care (De Laet and Dhondt 1989). Interestingly, we did not detect differences in feeding rate, suggesting that summarized parental care (female and male combined) per nestling was stable in both habitats during the breeding season. Also, reduced brood size for second broods seems to be a successful strategy of parents to maximize reproductive output when optimal nestling food is limited/declined. Parents' age can also impact parental success (Perrins and McCleery 2008). Older birds for example might be more experienced in searching for high quality food than first-year breeders. In our study, the proportion of young parents (< 2 years old) relative to the older parents in the two habitat types was similar (0.25 in both habitats, table 2s). This also supports the theory that, rather than parental experience, a limited food supply is the key factor regulating breeding success of great tits in our urban habitat.

Last but not least, our previous findings showed that our urban habitat is strongly food limited during first broods (Seress et al 2018, 2020; Sinkovics et al 2021). Our results from the present study strengthen and expand this earlier conclusion in that the shortage of optimal nestling food (caterpillars) in the cities is even more pronounced as the season progresses, presumably driving the reduced survival of urban nestlings we observed in second broods. Although urban great tit pairs try to compensate for the lack of caterpillars by reducing brood size and switching prey type, they likely cannot fully avoid the adverse effects of reduced food quality. Thus, as in our earlier studies, we suggest that improving urban habitat quality by supporting arthropod communities (for example by planting native trees, using fewer pesticides in parkland and garden management, reducing mowing intensity, and creating new habitats by sowing wildflowers; Süle et al 2023) would likely enhance the breeding success of urban insectivorous birds. We would thus like to encourage city managers to take these findings and suggestions into account when planning future urban parks.

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#### Author contributions

The study was conceived by C. Sinkovics, A. Liker, and G. Seress. Field data (breeding biology and video recordings) was collected by all authors. Data collection from the video recordings: C. Sinkovics. Statistical analyses: C. Sinkovics with input from all authors. Data visualisation: C. Sinkovics. All authors took parts in writing the manuscript.

#### Conflicts of interest

No conflicts declared

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## Supplementary material

**Table 1s.** Median and range (in brackets) hatching dates (day/month) of the video-recorded broods. The number of video-recorded broods is provided for each site (N).

**Tabla 1s.** Mediana e intervalo (entre paréntesis) de las fechas de eclosión (día y mes) de los pollos grabados en vídeo. Se proporciona el número de pollos grabados en vídeo de cada sitio (N).

	2014		2015		2016	
	First brood	Second brood	First brood	Second brood	First brood	Second brood
Szentgál	17/04 (17-18/04) N = 3	22/05 (21-25/05) N = 3	- N = 0	- N = 0	02/05 (30/04-04/05) N = 5	07/06 (06-12/06) N = 5
Vilma-puszta	21/04 (21-22/04) N = 2	27/05 (27-28/05) N = 2	- N = 0	- N = 0	- N = 0	- N = 0
Balatonfüred	14/04 (-) N = 1	30/05 (-) N = 1	14/04 (-) N = 1	30/05 (-) N = 1	14/04 (14-24/04) N = 3	28/05 (27/05-16/06) N = 3
Veszprém	13/04 (11-18/04) N = 5	03/06 (20/05-09/06) N = 5	- (02-05/05) N = 2	- (21-25/06) N = 2	24/04 (17-28/04) N = 10	10/06 (03-21/06) N = 10

**Table 2s.** Age structure of the video-recorded parents in each habitat and site. 'Young' refers to 1-year-old parents (hatched in the previous year), 'Older' refers to parents older than 2 years (i.e., having at least one breeding season before the current one). Fisher's exact test indicated no statistically significant difference between the distribution of the two age groups in the two habitat types (forest vs. urban;  $p = 1.000$ ).

**Tabla 2s.** Estructura por edad de los progenitores grabados en vídeo en cada hábitat y sitio. "Young" se refiere a los progenitores de un año de edad (nacidos el año anterior) y "Older" se refiere a los progenitores de más de dos años de edad (es decir, los que ya han vivido al menos una temporada de cría antes de la presente). La prueba exacta de Fisher determinó que no existían diferencias estadísticamente significativas entre la distribución de los dos grupos de edad en los dos tipos de hábitat (forestal y urbano;  $p = 1,000$ ).

	Young	Older
Forest habitat	4	16
Szentgál	3	13
Vilma-puszta	1	3
Urban habitat	9	35
Balatonfüred	6	4
Veszprém	3	31

**Table 3s.** Maximum brood size (mean  $\pm$  SE) at each study site. Maximum brood size was estimated as the maximum number of potentially hatched nestlings in a brood (calculated as the maximum number of eggs observed in the nest minus unhatched and broken eggs).

**Tabla 3s.** Tamaño máximo de la puesta (media  $\pm$  DE) en cada sitio del estudio. El tamaño máximo de la puesta se calculó como el número máximo de huevos que podrían haber eclosionado en una puesta (calculado como el número máximo de huevos observados en el nido menos los que no hubieran eclosionado y los rotos).

	2014		2015		2016	
	First brood	Second brood	First brood	Second brood	First brood	Second brood
Szentgál	10 $\pm$ 0.58	8.3 $\pm$ 0.67	-	-	10.8 $\pm$ 0.37	6.6 $\pm$ 1.17
Vilma-puszta	11 $\pm$ 0.00	8.5 $\pm$ 0.5	-	-	-	-
Balatonfüred	11	8	9	4	7.33 $\pm$ 1.67	6.33 $\pm$ 2.19
Veszprém	9.6 $\pm$ 0.93	8 $\pm$ 0.77	9 $\pm$ 0.00	6.5 $\pm$ 0.5	8.5 $\pm$ 0.54	6.6 $\pm$ 0.22