

# A comparison of the diet of urban and forest great tits in a Mediterranean habitat

J. C. Senar, A. Manzanilla, D. Mazzonei

Senar, J. C., Manzanilla, A., Mazzonei, D., 2021. A comparison of the diet of urban and forest great tits in a Mediterranean habitat. *Animal Biodiversity and Conservation*, 44.2: 321–327, Doi: <https://doi.org/10.32800/abc.2021.44.0321>

## Abstract

*A comparison of the diet of urban and forest great tits in a Mediterranean habitat.* The low breeding performance and body condition of nestling passerine birds in urban environments has been attributed to the poor quality and low abundance of food in these settings. However, detailed data on prey provided by parents to their chicks in the urban habitat is scarce. Here we used video cameras set in nest boxes to compare the diet of urban and forest great tits *Parus major* when provisioning their chicks in a Mediterranean area. We additionally analysed brood size and fledgling success. Breeding success of urban great tits was lower than that of forest birds. Urban parents displayed a lower average hourly feeding rate per nestling than forest parents. Among the three prey item categories, the percentage of spiders did not vary according to habitat. However, the percentage of caterpillars delivered to the nest by great tit parents was higher in the forest than in the urban habitat while the percentage of 'other' prey showed a reverse pattern. 'Other' prey were mainly adult butterflies and wasps in the urban habitat. Our paper adds to the view that the low feeding rates and scarcity of caterpillars in urban environments may be the underlying cause constraining the growth of great tit nestlings in these areas.

Key words: Urbanization, Diet, Great tits, Parental provisioning, Prey composition, Prey size

## Resumen

*Comparación de la dieta de los carboneros comunes en entornos urbanos y forestales en un hábitat mediterráneo.* El escaso éxito reproductor y la condición física deficiente de los pollos de paseriformes en entornos urbanos se han atribuido a la escasez de alimentos en estos ambientes y a la mala calidad de estos. No obstante, existen pocos datos detallados sobre las presas que los progenitores llevan a sus pollos en el hábitat urbano. En este estudio, empleamos videocámaras instaladas en cajas nido con objeto de comparar la dieta que los carboneros comunes, *Parus major*, del medio urbano y forestal proporcionan a sus pollos en una zona del Mediterráneo. Asimismo, analizamos el tamaño de la nidada y el éxito de los volantones. El éxito reproductor de los carboneros comunes del medio urbano fue inferior al de las aves forestales. Se observó que la tasa media de alimentación por hora y por nidada de los progenitores del medio urbano fue inferior a la de los progenitores del medio forestal. Entre las tres categorías de presas, el porcentaje de arañas no varió en función del hábitat. Sin embargo, el porcentaje de orugas que los progenitores de carbonero común llevaron a los nidos fue mayor en el bosque que en el hábitat urbano, mientras que el porcentaje de "otras" presas mostró la pauta inversa. En el hábitat urbano, la categoría "otras" presas estuvo principalmente compuesta por mariposas y avispas adultas. Nuestro artículo se suma a la opinión de que las tasas de alimentación bajas y la escasez de orugas en los entornos urbanos pueden ser los factores que limitan el crecimiento de los pollos de carbonero común en estas zonas.

Palabras clave: Urbanización, Dieta, Carboneros comunes, Aprovisionamiento parental, Composición de las presas, Tamaño de las presas

Received: 21 VI 21; Conditional acceptance: 2 IX 21; Final acceptance: 20 IX 21

J. C. Senar, A. Manzanilla, D. Mazzonei, Museu de Ciències Naturals de Barcelona, Parc Ciutadella, Passeig Picasso s/n., 08003 Barcelona, España (Spain).

Corresponding author: J. C. Senar. E-mail: [jcsenar@bcn.cat](mailto:jcsenar@bcn.cat)

ORCID ID: J. C. Senar: 0000-0001-9955-3892; D. Mazzonei: 0000-0001-7342-4857



## Introduction

Breeding performance and nestling body composition in birds in urban environments are inferior to those in birds in more natural habitats (Solonen, 2001; Chamberlain et al., 2009; Bailly et al., 2016; Demeyrier et al., 2016; Seress et al., 2018). According to the food limitation hypothesis (Newton, 1998), food shortage and low food quality in urban environments may be a main proximate reason for the lower breeding success in urban passerine populations (Eeva et al., 1997; Robb et al., 2008; Remacha and Delgado, 2009; Seress et al., 2018).

Analyses of prey composition delivered by parents to their chicks comparing forest and urban insectivorous birds stress that forest parents provide a higher proportion of caterpillars to their chicks than urban parents (Riddington and Gosler, 1995; Pollock et al., 2017; Seress et al., 2018). Urban birds seem instead to rely mostly on adult Diptera, Coleoptera or Aranea (Riddington and Gosler, 1995). However, except for this paper, data on alternative prey delivered by parents to their chicks in the urban habitat are scarce.

Food supplementation experiments should be a good approach to solve whether the lower breeding success of urban birds is due to a limitation in the quantity or quality of food collected by urban birds. However, food supplementation experiments in urban birds have found positive (Bañura et al., 2011; Seress et al., 2020), negligible (Meyrier et al., 2017), and even negative (Demeyrier et al., 2017) impact on body size and/or nestling survival. It is therefore unclear the extent to which reductions in breeding success of urban birds are driven by a reduced abundance of natural 'high quality' dietary components. As stated by Demeyrier et al. (2017), further detailed knowledge on the diet of passerine birds in cities is needed.

The aim of this paper was to compare the breeding success and diet of urban and forest great tits *Parus major* in a Mediterranean locality, and to analyse in detail the composition of prey delivered by urban great tit parents to their chicks. We used a digital micro-camera attached to the nest-box roof and focused on the entrance so as to record delivered prey. We focused on the great tit because it is a clear model species in studies of the effects of urbanization on breeding ecological parameters (see previous references).

## Material and methods

We analysed the breeding success and diet of great tit nestlings in an urban habitat and in a forest habitat during the breeding season in 2018 and 2019. Forest data were collected at the Can Catà field station, located in the Collserola Natural Park (Cerdanyola, Barcelona, 90 NE of the Iberian Peninsula, 45° 27' N, 2° 8' E). At this location there were a total of 182 nest boxes. Urban birds were studied in three sub-urban parks in the city of Barcelona: Sentmenat, Laberint d'Horta and Desert de Sarrià (see Björklund et al., 2010 for details on the location of the parks). We

placed 14 nest boxes in Sentmenat, 12 in Laberint d'Horta and 8 in Desert de Sarrià. The forest area is 3 km from Laberint d'Horta and about 7 km from Sentmenat and Sarrià.

We visited nest boxes 2–3 times a week during the reproduction season in order to control the construction status of the nests and to determine laying date and clutch size. Hatching date was determined from daily nest checks starting 2 days before the expected hatch date. Once the hatching date was determined, the nests were visited as little as possible until the day of recording to minimize the negative effects of human presence. We ringed nestlings at 14–17 days old (around five days before fledging), and posterior checkings allowed to determine fledging success as number of chicks abandoning successfully the nest.

Data on clutch size and on fledging success was analyzed with GLM, including factor habitat (forest/city) and also year (2018/2019) to standardize for its effect.

A digital micro-camera (Mini Colour Sony IR Camera SK-C170IR) attached to the nest-box roof was located and focused on the entrance, so that delivered prey could be observed. These cameras have an infrared vision and a motion sensor. The cameras were installed on an afternoon when the chicks were between 7 and 13 days old (with a median age of 9 days old), and continuous recordings were made until at least 12 p.m. the next day. The afternoon of the first day was excluded from the analyses so as to accustom the birds to the presence of the camera. We counted the nestlings again when we installed the video camera. We did not observe any desertion because of the presence of the camera. We used the 5-hour recording of the second day, from 7:00 a.m. to 12:00 p.m., to collect the data concerning diet (Pagani-Núñez and Senar, 2013). Recordings were obtained from 29 of April to 30 of June, thus being representative of the whole breeding season.

Once all boxes were recorded, the videos were analysed ( $n = 83$  forest,  $n = 10$  city). To avoid any bias, all the videos were analyzed by the same person (AM). We determined the parents' sex, prey type, prey size, and exact time for each feeding action using Micro D Player software. To differentiate males from females, we used the shininess of the black cap, which is glossier in males. This sexual dichromatism is accentuated under infrared light (Pagani-Núñez and Senar, 2014). We classified prey into three categories: caterpillars, spiders, and 'others'. The 'others' included Hymenoptera, Coleoptera, Orthoptera, Phasmida, Diptera, fruits and other unidentified prey. 'Artificial' food was not detected, and we should stress that it is rare for people in Barcelona to have bird tables. In our area it also seems that great tits do not use bird feeders when they are rearing chicks. Although not all prey could be clearly identified, we were able to categorise around 90% of the prey. Prey size was estimated in relation to the length of the bill (average 9 mm) and according to a semi-quantitative scale: small (less than 9 mm), medium (9.1 mm–12 mm) and large (longer than 12.1 mm) (García-Navas and Sanz, 2010; Pagani-Núñez et al., 2011).

We computed the absolute number of total feeding actions brought by each parent to each nest box. In most (99%) of the feeding actions, parents brought a single prey. We thus assume one prey per visit when estimating the number of prey per hour. Feeding rate (number of prey per hour per nestling) was used as a dependent variable in a general linear model (GLM). We used a natural logarithm transformation to fit the dependent variable to a normal distribution and homogenize its variance (Guisande González et al., 2013). Variables sex, habitat and year were used as categorical variables and date (days from April 1st) and the age of the chicks (in days) during videotaping as continuous variables. Sex, year, date and the age of the chicks were added into analyses to control for their effect when analysing habitat differences. We tried to add nest box identification as a random factor, to control for the effect that each nest box appeared twice (for the male and for the female), but this resulted in a over-parameterized model, so we decided not to include this variable. This was also the case with the next analyses. Prey composition was also analysed through a multiple general linear model (MGLM). Prey composition, taken as the percentage of the three main prey types, was logit transformed (Guisande González et al., 2013). Variables sex, habitat and year were used as categorical variables and date (days from April 1st), age of the chicks (in days) during videotaping, and the number of chicks in the nest were used as continuous variables. The average size of each of the groups of prey brought to each nest box was similarly analyzed using an MGLM, where sex, habitat and year were the categorical variables and date, number of chicks in the nest, and their age were the continuous variables.

The specific composition of 'other' prey in the urban area was computed for each nest box and values then were averaged. In this analyses we added data from a nest box recorded in 2015 in Desert de Sarria. This nest box was not included in the previous analyses because we had only one nest box and this would not allow to include factor year in analyses. Prey composition of that nestbox was similar to that of other urban nestboxes recorded in 2018 and 2019, not biasing results but allowing to increase sample size.

Mean values are provided with  $\pm$  S.E.

## Results

Clutch size was larger in the forest than in the city (forest:  $8.2 \pm 0.11$  SE eggs; city:  $6.4 \pm 0.46$ ;  $F_{1,236} = 13.48$ ,  $p < 0.001$ ). The number of fledglings successfully leaving the nest did not differ between the forest and the city when taking into account abandoned nests or nests in which chicks died from starvation (i.e. breeding success = 0) (forest:  $4.3 \pm 0.20$  fledglings; city:  $3.9 \pm 0.90$ ;  $F_{1,204} = 0.24$ ,  $p = 0.62$ ). However, considering only nests where at least one chick fledged, the number of fledglings successfully leaving the nest was higher for the forest than for the city (forest:  $6.0 \pm 0.17$  fledglings; city:  $4.2 \pm 0.73$ ;  $F_{1,136} = 5.59$ ,  $p < 0.05$ ).

Table 1. GLM analysis of the variation in provisioning rate (chick /hour) according to habitat (urban vs. forest), date (days from 1st April), age of the chicks (in days), sex of the parents and year (2018 or 2019). Year was included as a random factor.

*Tabla 1. Análisis mediante un modelo lineal generalizado de la variación de la tasa de aprovisionamiento (por pollo y por hora) según el hábitat (urbano o forestal), la fecha (días a partir del 1 de abril), la edad de los pollos (en días), el sexo de los progenitores y el año (2018 o 2019). El año se incluyó como factor aleatorio.*

	$\beta$	$F$	$p$
Habitat	0.18	7.62	< 0.01
Chick age	0.06	0.95	0.33
Parent sex	0.09	1.81	0.18
Date	-0.42	41.52	< 0.001
Year	-0.39	36.95	< 0.001

Urban parents displayed a lower average hourly feeding rate per nestling than forest parents (urban:  $1.26 \pm 0.32$ ; forest:  $2.28 \pm 0.11$  feedings/chick/hour; mean  $\pm$  SE) (table 1). The chick provisioning rate was not affected by the age of the chicks or the sex of the parents (table 1). The feeding rate decreased significantly over the season, and in 2019 the feeding rate was higher than that in 2018 (sites combined) (table 1). The median number of prey items provided by an individual during the 5 hours of recording was 59 (range 8–195) for the forest habitat and 27 (range 8–58) for the urban habitat.

The percentage of caterpillars delivered to the nest by great tit parents was higher in the forest ( $0.70 \pm 0.02$ ) than in the urban habitat ( $0.42 \pm 0.04$ ) (table 2, fig. 1). The median number of caterpillars provided by an individual in the five hours in which they were recorded was 38 (range 2–185) in the forest and 8 (range 0–29) in the city. The percentage of caterpillars also increased with the age of the chicks, and brood size, and was higher in 2018 than in 2019 (table 2). Date and sex of parents had no significant effect (table 2). The percentage of 'other' prey delivered to the nest by great tit parents was lower in the forest ( $0.24 \pm 0.01$ ) than in the urban habitat ( $0.49 \pm 0.04$ ) (table 2, fig. 1). The median number of 'other' prey provided by an individual was 8 (range 0–110) in the forest and 12 (range 3–43) in the city. The percentage of spiders did not vary according to habitat ( $0.06 \pm 0.01$  vs.  $0.08 \pm 0.01$ ) and was only affected by brood size (higher in smaller broods) and year (higher in 2018). The median number of spiders provided by an individual was 3 (range 0–28) in the forest and 2 (range 0–8) in

Table 2. MGLM analysis comparing the percentage (ln transformed) of caterpillars, spiders and 'other' prey according to date, age of the chicks (in days), brood size, habitat (forest vs. city), year (2018 or 2019) and sex of the parents.

Tabla 2. Análisis mediante un modelo lineal generalizado multivariante para comparar el porcentaje (transformado logarítmicamente) de orugas, arañas y "otras" presas en función de la fecha, la edad de los pollos (en días), el tamaño de la nidada, el hábitat (forestal o urbano), el año (2018 o 2019) y el sexo de los progenitores.

	Caterpillars			Spiders			Other		
	$\beta$	$t$	$p$	$\beta$	$t$	$p$	$\beta$	$t$	$p$
Date	0.01	0.12	0.91	0.00	0.01	0.99	0.05	0.68	0.50
Chick age	0.20	2.78	<0.01	-0.16	-1.93	0.06	-0.18	-2.64	<0.01
Brood size	0.26	2.69	<0.01	-0.26	-2.28	0.02	-0.25	-2.76	<0.01
Habitat	-0.22	3.02	<0.01	0.15	-1.79	0.08	0.20	-2.83	<0.01
Year	-0.23	2.55	<0.01	-0.37	3.49	<0.001	0.36	-4.18	<0.001
Parent sex	-0.11	-1.60	0.11	0.15	1.84	0.07	0.08	1.18	0.24

the city. Other prey in the urban habitat consisted mainly of Lepidoptera (butterflies, 50%  $\pm$  12.1) and Hymenoptera (31%  $\pm$  12.0) adults, and to a lesser extent to Orthoptera (11%  $\pm$  8.0) and Diptera adults (8%  $\pm$  4.4).

Caterpillar size and 'other' prey size did not vary according to habitat. Average spider size was larger in the city than in the forest (forest: 2.4  $\pm$  0.05; city: 2.5  $\pm$  0.13) (table 3). Caterpillar size increased throughout the season, was larger in larger broods and larger in 2018. 'Other' prey size also increased over the season and was also larger in 2018 (table 3). Females provided larger spiders than males, and spider size was also larger in 2018 (table 3).

## Discussion

Our paper supports previous data indicating that the productivity of urban great tits is lower than that of their forest counterparts (Solonen, 2001; Chamberlain et al., 2009; Bailly et al., 2016; Demeyrier et al., 2016; Seress et al., 2018). Our analyses also showed that the prey composition of parents provisioning nestlings in the forest habitat in Barcelona was dominated by caterpillars (70% of all delivered prey). This contrasted with data from the urban habitat where caterpillars made up only 42% of delivered prey. 'Other' prey followed the reverse pattern, with 24% of delivered prey in the forest being 'other' insects, while values increased to 49% in the urban area. We acknowledge that our sample size was low for the city area, but despite the low power the effect sizes were large. Our results are fundamentally similar to data from other studies where caterpillars are the main prey in forests and adult stages of other insect groups constitute a great percentage of prey delivered in

urban areas (Riddington and Gosler, 1995; Pollock et al., 2017). Data from Barcelona have shown that alternative prey in the city were mainly butterflies, wasps and grasshoppers, findings that differ from those in Britain, where 'other' prey mainly consisted of beetles and flies (Riddington and Gosler, 1995). This difference is probably related to the relative abundance of different prey between areas, acknowledging that different urban areas may differ in the relative proportion of 'green' areas, plant composition, and managing practices, so that availability of types of prey may differ greatly between cities.

In relation to the size of the prey, we did not find differences between the forest and the urban habitat. This contrasts with data from blue tits *Cyanistes caeruleus* in Glasgow, where caterpillars provided to chicks in the forest area were larger than those in the urban area (Pollock et al., 2017) and data from house sparrows *Passer domesticus* in Hungary, where rural house sparrow parents provided larger prey items than urban parents (Seress et al., 2012). In contrast, the length of caterpillar prey provided by great tit parents in Belgium did not vary with urbanization (Satgé, 2016), similarly to our data from Barcelona. Again, the difference between studies is probably related to the relative abundance of different prey sizes in different areas.

When analysing feeding rates, we found that urban parents in Barcelona displayed a lower average hourly feeding rate per nestling than forest parents. This result is similar to that observed in starlings *Sturnus vulgaris* where nestlings in the city center received less food (Mennechez and Clergeau, 2006). However, provisioning rates in great tits in Belgium were not found to vary with urbanization (Satgé, 2016), and data from blue tits in Glasgow and great tits in Sweden showed the reverse pattern, with urban

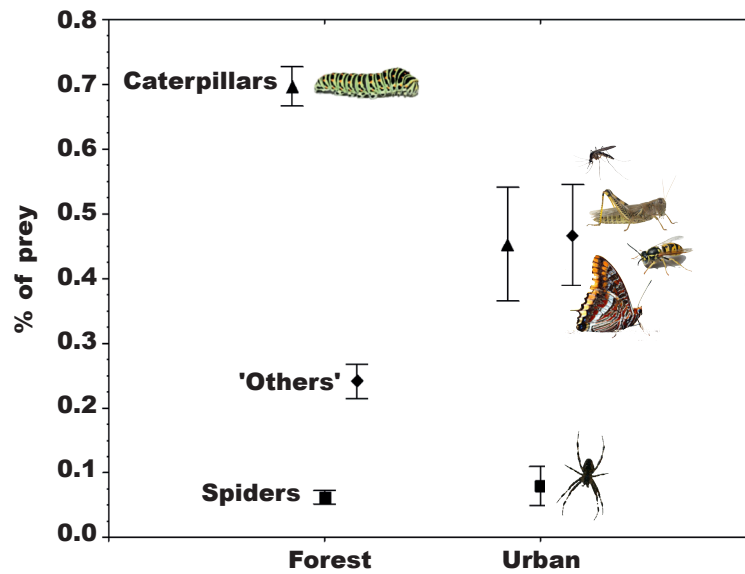


Fig. 1. Proportions of different prey provided by great tits to chicks according to forest or urban habitat. The most abundant food provided in the forest environment was caterpillars, followed by the 'others' group, and finally, spiders. In the urban environment, the proportion of caterpillars decreased significantly compared to forest habitat and the proportion of 'others' increased. The abundance of spiders did not vary significantly. Sample size of nests: forest N = 83, city N = 10.

Fig. 1. Proporción de las distintas presas proporcionadas por los carboneros comunes a los pollos según el hábitat sea forestal o urbano. El alimento más abundante en el entorno forestal fueron las orugas, seguidas de "otras" presas y por último, de las arañas. En el entorno urbano, la proporción de orugas descendió significativamente en comparación con el hábitat forestal y la proporción de "otras" presas aumentó. La abundancia de arañas no varió de forma significativa. Tamaño de la muestra de nidos: bosque (N = 83), ciudad (N = 10).

Tabla 3. MGLM analysis of the variation in the size of caterpillars, spiders and 'other' prey provided by great tit parents to their chicks. Variation is analyzed according to date (days from 1st April), age of the chicks, brood size, habitat (forest vs. Urban), year (2018 or 2019) and sex of the parents.

Tabla 3. Análisis mediante un modelo lineal generalizado multivariante de la variación del tamaño de las orugas, las arañas y "otras" presas proporcionadas por los progenitores de carbonero común a sus pollos. La variación se analiza en función de la fecha (días a partir del 1 de abril), la edad de los pollos, el tamaño de la nidada, el hábitat (forestal o urbano), el año (2018 o 2019) y el sexo de los progenitores.

	Caterpillars			Spiders			Other		
	$\beta$	$t$	$p$	$\beta$	$t$	$p$	$\beta$	$t$	$p$
Date	0.38	5.73	<0.001	0.12	1.59	0.11	0.27	3.41	<0.001
Chick age	0.08	1.21	0.23	0.06	0.79	0.43	0.09	1.13	0.26
Brood size	0.18	2.00	< 0.05	0.08	0.76	0.45	-0.03	-0.27	0.79
Habitat	0.05	-0.79	0.43	0.21	-2.70	<0.01	0.09	-1.1	0.27
Year	-0.51	6.14	<0.001	-0.44	4.55	<0.001	-0.39	3.94	<0.001
Parent sex	-0.04	-0.67	0.50	0.2	2.75	<0.01	-0.14	-1.8	0.07

nestlings being fed more often than forests nestlings (Isaksson and Andersson, 2007; Pollock et al., 2017). Differences between studies could perhaps be due to differences in traveling distances across different areas when provisioning their nestlings (Demeyrier et al., 2017). This difference could also be the result of the trade-off between prey size and feeding rates: when meals provided by parents include large prey, the number of trips is lower, and when prey are small, the number of trips is higher (Grieco, 2001, 2002; Navalpotro et al., 2016).

To conclude, our paper adds to the growing view that the diet of insectivorous nestlings in urban areas is deficient in caterpillars. This may be the reason underlying reduced breeding success in the urban habitat (Bañbura et al., 1999; Pollock et al., 2017; Seress et al., 2018). However, without more exact nutritional data regarding the various species of prey items provided to nestlings it is not clear whether a combination of other insects and related arthropods could fulfill the nutritional requirements of insectivorous birds in urban habitats. We therefore urge urban ecologists to analyze in detail the nutritional profile of the diet of urban and forest insectivorous birds in order to understand why, as suggested (see above), caterpillars, and only caterpillars, can make the difference.

## Acknowledgements

We are most grateful to Mark Finke for reviewing the paper. We also thank Lluisa Arroyo, Helena Navalpotro and Xavier Altarriba for their help in the field and in the lab. We thank the Gil family, owners of Can Catà, for allowing us to work on their property. Birds were handled with the permission of the Departament de Medi Ambient, Generalitat de Catalunya (SF/542). The Catalan Institute of Ornithology (ICO) provided the rings. This work was supported by funds from the Ministry of Economy and Competitiveness, Spanish Research Council to JCS (CGL-2016-79568-C3-3-P).

## References

- Bailly, J., Scheifler, R., Berthe, S., Clément-Demange, V.-A., Leblond, M., Pasteur, B., Faivre, B., 2016. From eggs to fledging: negative impact of urban habitat on reproduction in two tit species. *Journal of Ornithology*, 157(2): 377–392, Doi: [10.1007/s10336-015-1293-3](https://doi.org/10.1007/s10336-015-1293-3)
- Bañbura, J., Bañbura, M., Gladalski, M., Kalinski, A., Markowski, M., Michalski, M., Nadolski, J., Skwarska, J., Zielinski, P., 2011. Body Condition Parameters of Nestling Great Tits *Parus major* in Relation to Experimental Food Supplementation. *Acta Ornithologica*, 46(2): 207–212, Doi: [10.3161/000164511X625991](https://doi.org/10.3161/000164511X625991)
- Bañbura, J., Lambrechts, M. M., Blondel, J., Perret, P., Cartan-Son, M., 1999. Food Handling Time of Blue Tit Chicks: Constraints and Adaptation to Different Prey Types. *Journal of Avian Biology*, 30(3): 263–270, Doi: <https://doi.org/10.2307/3677352>
- Björklund, M., Ruiz, I., Senar J. C., 2010. Genetic differentiation in the urban habitat: the great tits (*Parus major*) of the parks of Barcelona city. *Biological Journal of the Linnean Society*, 99(1): 9–19, Doi: [10.1111/j.1095-8312.2009.01335.x](https://doi.org/10.1111/j.1095-8312.2009.01335.x)
- Chamberlain, D. E., Cannon, A. R., Toms, M. P., Leech, D. I., Hatchwell, B. J., Gaston, K. J., 2009. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis*, 151: 1–18, Doi: <https://doi.org/10.1111/j.1474-919X.2008.00899.x>
- Demeyrier, V., Charmantier, A., Lambrechts, M. M., Grégoire, A., 2017. Disentangling drivers of reproductive performance in urban great tits: A food supplementation experiment. *The Journal of Experimental Biology*: 161067, <http://jeb.biologists.org/content/early/2017/09/21/jeb.161067>
- Demeyrier, V., Lambrechts, M. M., Perret, P., Grégoire, A., 2016. Experimental demonstration of an ecological trap for a wild bird in a human-transformed environment. *Animal Behaviour*, 118: 181–190.
- Eeva, T., Lehikoinen, E., Pohjalainen, T., 1997. Pollution-related variation in food supply and breeding success in two hole-nesting passerines. *Ecology*, 78: 1120–1131.
- García-Navas, V., Sanz, J. J., 2010. Flexibility in the Foraging Behavior of Blue Tits in Response to Short-Term Manipulations of Brood Size. *Ethology*, 116(8): 744–754, Doi: [10.1111/j.1439-0310.2010.01788.x](https://doi.org/10.1111/j.1439-0310.2010.01788.x)
- Grieco, F., 2001. Short-term regulation of food-provisioning rate and effect on prey size in blue tits, *Parus caeruleus*. *Animal Behaviour*, 62(1): 107–116, Doi: [10.1006/anbe.2001.1736](https://doi.org/10.1006/anbe.2001.1736)
- 2002. Time constraint on food choice in provisioning blue tits, *Parus caeruleus*: the relationship between feeding rate and prey size. *Animal Behaviour*, 64(4): 517–526, Doi: [10.1006/anbe.2002.3073](https://doi.org/10.1006/anbe.2002.3073)
- Guisande González, C., Vaamonde Liste, A., Barreiro Felpeo, A., 2013. *Tratamiento de datos con R, Estadística y SPSS*. Ediciones Díaz de Santos, Madrid.
- Isaksson, C., Andersson, S., 2007. Carotenoid diet and nestling provisioning in urban and rural great tits *Parus major*. *Journal of Avian Biology*, 38: 564–572, Doi: [10.1111/j.2007.0908-8857.04030.x](https://doi.org/10.1111/j.2007.0908-8857.04030.x)
- Mennechez, G., Clergeau, P., 2006. Effect of urbanisation on habitat generalists: starlings not so flexible? *Acta Oecologica*, 30: 182–191, Doi: [10.1016/j.actao.2006.03.002](https://doi.org/10.1016/j.actao.2006.03.002)
- Meyrier, E., Jenni, L., Bötsch, Y., Strebel, S., Erne, B., Tablado, Z., 2017. Happy to breed in the city? Urban food resources limit reproductive output in Western Jackdaws. *Ecology and Evolution*, 7(5): 1363–1374, Doi: [10.1002/ece3.2733](https://doi.org/10.1002/ece3.2733)
- Navalpotro, H., Pagani-Núñez, E., Hernández-Gómez, S., Senar, J. C., 2016. Comparing prey composition and prey size delivered to nestlings by great tits, *Parus major*, and blue tits, *Cyanistes caeruleus*, in a Mediterranean sclerophyllous mixed forest. *Animal Biodiversity and Conservation* 39:129–139, Doi: [10.32800/abc.2016.39.0129](https://doi.org/10.32800/abc.2016.39.0129)
- Newton, I., 1998. *Population limitation in birds*. Academic Press, San Diego.
- Pagani-Núñez, E., Ruiz, I., Quesada, J., Negro, J. J., Senar, J. C., 2011. The diet of Great Tit *Parus major* nestlings in a Mediterranean Iberian forest: the

- important role of spiders. *Animal Biodiversity and Conservation*, 34: 355–361.
- Pagani-Núñez, E., Senar, J. C., 2013. One hour of sampling is enough: Great Tit *Parus major* parents feed their nestlings consistently across time. *Acta Ornithologica*, 48(2): 194–200, Doi: [10.3161/000164513X678847](https://doi.org/10.3161/000164513X678847)
- 2014. Are colorful males of great tits *Parus major* better parents? Parental investment is a matter of quality. *Acta Oecologica*, 55: 23–28, Doi: [10.1016/j.actao.2013.11.001](https://doi.org/10.1016/j.actao.2013.11.001)
- Pollock, C. J., Capilla-Lasheras, P., McGill, R. A. R., Helm, B., Dominoni, D. M., 2017. Integrated behavioural and stable isotope data reveal altered diet linked to low breeding success in urban-dwelling blue tits (*Cyanistes caeruleus*). *Scientific Reports*, 7: 501, <http://www.nature.com/articles/s41598-017-04575-y>
- Remacha, C., Delgado, J. A., 2009. Spatial nest-box selection of cavity-nesting bird species in response to proximity to recreational infrastructures. *Landscape and Urban Planning*, 93(1): 46–53, Doi: [10.1016/j.landurbplan.2009.06.004](https://doi.org/10.1016/j.landurbplan.2009.06.004)
- Riddington, R., Gosler, A. G., 1995. Differences in reproductive success and parental qualities between habitats in the Great Tit *Parus major*. *Ibis*, 137(3): 371–378, Doi: [10.1111/j.1474-919X.1995.tb08035.x](https://doi.org/10.1111/j.1474-919X.1995.tb08035.x)
- Robb, G. N., McDonald, R. A., Chamberlain, D. E., Bearhop, S., 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment*, 6(9): 476–484, Doi: [10.1890/060152](https://doi.org/10.1890/060152)
- Satgé, J. de, 2016. Urban Areas as Ecological Traps: Studying Great Tits *Parus Major* Along an Urbanisation Gradient. Master thesis, University of Antwerp, Doi: [10.13140/RG.2.2.29551.74409](https://doi.org/10.13140/RG.2.2.29551.74409)
- Seress, G., Bókony, V., Pipoly, I., Szép, T., Nagy, K., Liker, A., 2012. Urbanization, nestling growth and reproductive success in a moderately declining house sparrow population. *Journal of Avian Biology*, 43(5): 403–414, Doi: [10.1111/j.1600-048X.2012.05527.x](https://doi.org/10.1111/j.1600-048X.2012.05527.x)
- Seress, G., Hammer, T., Bókony, V., Vincze, E., Preiszner, B., Pipoly, I., Sinkovics, C., Evans, K. L., Liker, A., 2018. Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. *Ecological Applications*, 28(5): 1143–1156. Doi: [10.1002/eap.1730](https://doi.org/10.1002/eap.1730)
- Seress, G., Sándor, K., Evans, K. L., Liker, A., 2020. Food availability limits avian reproduction in the city: An experimental study on great tits *Parus major*. *Journal of Animal Ecology*, 89(7): 1570–1580, Doi: [10.1111/1365-2656.13211](https://doi.org/10.1111/1365-2656.13211)
- Solonen, T., 2001. Breeding of the Great Tit and Blue Tit in urban and rural habitats in southern Finland. *Ornis Fennica*, 78: 49–60.
-

