THESES OF DOCTORAL (PHD) DISSERTATION

HABITAT AND SEASONAL DIFFERENCES IN THE DIET OF GREAT TIT *(PARUS MAJOR)* NESTLINGS

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1. INTRODUCTION

Currently over half of the human population lives in cities and the increasing trend of urbanization is expected to continue in the foreseeable future (United Nations, Report 2022/11). Transforming natural habitats into urbanized areas poses a challenge for wildlife due to the altered environmental conditions. One common trend observed in urban passerines (order *Passeriformes*) is the inferior breeding success compared to their rural counterparts which results in smaller clutch sizes, smaller nestling weight and smaller nestling survival (Seress et al. 2018; Capilla-Lasheras et al. 2022). According to the food-limitation hypothesis the reduced availability of high-quality food for nestlings is the major driver of the reduced reproductive success in urban areas (Chamberlain et al. 2009; Seress and Liker 2015; Bailly et al. 2016). For many insectivorous birds, it is known that lepidopteran larvae (caterpillars) are the primary nestling food in natural habitats in the temperate climate zone (Perrins 1991; Krištín and Patočka 1997). Caterpillars are widely preferred prey items of songbirds for several reasons. First, caterpillars have especially high nutritional value as they are rich in proteins (Ramsay and Houston 2003) and lipids (Lease and Wolf 2011). Second, caterpillars have soft bodies, which makes them easily digestible for young birds, which is essential given that nestlings have poorer digestive capabilities than adult birds (Caviedes-Vidal and Karasov 2001). Third, caterpillars also contain large amounts of carotenoids which compounds serve various functions in birds, for example, they act as antioxidant and they have important role in developing plumage colour (Blount et al. 2003). Fourth, caterpillars are highly abundant in a specific period called ’caterpillar peak’. This time they are found in high amount on plants, trees, and shrubs, providing birds with a consistent and easily accessible food supply. The importance of caterpillar biomass at the breeding time of birds is widely documented in migratory bird species, who time their arrival to the local caterpillar peak (Verboven et al. 2001) whereupon mismatching the timing of breeding often leads to lower breeding success (Visser et al. 2004). For example, a study found that those pied flycatcher *(Ficedula hypoleuca)* populations that missed the caterpillar peak in their habitat have declined by about 90% (Both et al. 2006). Further evidence for the food limitation hypothesis is that studies which documented poor caterpillar availability in certain habitats such as evergreen forests, agricultural areas, etc., have often also documented inferior breeding success in birds (Bańbura et al. 1994).

Habitat and seasonal differences in caterpillar biomass

The processes associated with urbanization (e.g. altered, exotic vegetation and climatic conditions, pollutions) radically change urban arthropod communities. Although different arthropod taxa seem to exhibit heterogeneous responses to urbanization, a global meta-analysis revealed that terrestrial arthropod communities are less diverse and abundant with increased urbanization and that *Lepidoptera* is one of the most threatened group (Fenoglio et al. 2020). Those studies that compared caterpillar biomass between urban and forest habitats found clear evidence for the substantial decrease in peak caterpillar abundance in cities and long-term studies highlighted yearly variation in the degree of this difference (Pollock et al. 2017; Seress et al. 2018; Nadolski et al. 2021). For example, in our urban and forest habitats where my PhD research was conducted we found two main features of caterpillar biomass that differ between the two habitat types. First, caterpillar biomass was significantly lower in urban than in forest habitats throughout the studied years (8.5 to 24 times difference; Seress et al. 2018). Second, the forest habitats were characterized by a single large massive caterpillar biomass peak during the nestling rearing period of the first broods and the biomass strongly decreased until the breeding season ended. In contrast, in urban habitats we also observed a seasonal decline of caterpillars in some but not all years and/or sites, but this decline was less pronounced because urban trees exhibited several small caterpillar peaks throughout the breeding season (Figre I. 1B; Seress et al. 2018). Based on the above results and in line with the food limitation hypothesis, the reduced availability of caterpillars and their different seasonal dynamics observed in urban environment probably have detrimental effects on nestling development throughout their diet which may contribute to their lower condition and success.

Effects of urbanization on nestling diet

As discussed above, the connection between caterpillar abundance and breeding success has been the focus of intense research. However, nestling diet (i.e. food items that nestlings de facto consume) is less examined. Furthermore, earlier studies were often limited to one aspect of the nestling diet (amount or composition), despite the fact that these are both equally important from the point of view of the offspring's development. A sufficient amount of food is obviously necessary for the nestlings as they have high metabolic rates and rapid growth rates, thus, they require a substantial amount of energy and nutrients to develop their body tissues, feathers, and organs. In addition, sufficient food quality is just as important as food quantity since the lack of essential nutrients may lead to malnourishment, altered feather properties, and also induce oxidative stress in nestlings (Heiss et al. 2009; Eeva et al. 2010; Biard et al. 2017; Bernat-Ponce et al. 2023). There are several traditional diet sampling techniques, such as direct observation with binoculars (Seress et al. 2012), analysing the nestlings' blood/faecal samples (Orłowski et al. 2015; Kaliński et al. 2019), and all of these methods have their benefits and disadvantages. During my doctoral research, I used video recordings at the nest to identify nestling food. This method allowed me to simultaneously examine the feeding activity of the parents and the amount and composition of food brought to the nestlings, i.e. the quantitative and qualitative characteristics of the nestling food.

So far, there are relatively few studies that systematically examined both the composition and amount of nestling diet in relation to urbanization. Furthermore, the previous studies covered mostly one or two breeding seasons, despite the fact that there can be large year-to-year differences in caterpillar abundance between urban and natural habitats (Seress et al. 2018; Nadolski et al. 2021). Moreover, former studies usually were focusing on the first brood of a breeding pair exclusively, even though numerous insectivorous bird species breed multiple times within a season both in urban and in natural habitats. Since caterpillar peaks occur in a relatively short time interval, it is possible that nestlings hatched in second broods may develop under suboptimal food availability conditions, which may also lead to malnourished nestlings.

2. THESIS OBJECTIVES

In my doctoral studies, my general aim was to better understand the role of nestling diet in the breeding success of great tits by examining the chick-feeding behaviour of parents.

My aim was to answer the following questions:

1.) How accurate and repeatable are the food size data collected from video recordings?

2.) Do the composition and amount of nestling food differ in forest and urban great tit populations?

3.) Is there seasonal differences (between first and second broods) in the composition and quantity of nestling food within forest and urban great tit populations? Does the reproductive success of first and second broods differ in these populations?

3. METHODS

As a model organism, we studied the great tits *(Parus major)*, which is a small insectivorous passerine species occurring both in urban and forest habitats as well as it readily nests in artificial nest boxes. We carried out these studies in two urban (Veszprém and Balatonfüred) and two forest (Vilma-puszta and Szengtál) habitats in three consecutive years (2014, 2015, 2016). We checked the nest boxes at least every 3 to 4 days throughout each breeding season to determine laying dates, clutch sizes, hatching dates, brood sizes of breeding great tits. When the nestlings were 8-12 days old, we made one 60-minutes long video-recording at the nest to examine the nestling-feeding behaviour of parent birds. We put a camera (GoPRO Hero 2 and 3) into a black plastic box outside of the nest box, circa 15 cm from the entrance hole. These plastic boxes serve as camouflage for the cameras, and are constant accessories of our nest boxes; breeding birds are familiar with them (Seress et al. 2017). Earlier studies showed that this recording length is suitable for characterizing the variation in parental provisioning in great tits (Pagani-Núñez and Senar 2013) and differences between pairs are also detectable (Murphy et al. 2015). Before the recordings we counted the nestlings and recorded the time and actual temperature. To avoid disturbing the parents' behaviour the observers who mounted the cameras stayed away from the nest during the recording periods. We ringed the parents with a unique combination of a numbered metal ring and three plastic colour rings and determined their sex and age based on their plumage coloration (Svensson 1992). We also measured their left tarsus length, wing length and body mass. Nestlings were also ringed with a numbered metal ring and measured with the same process circa a week prior to fledging (i.e. 14-17 days after hatching). We never captured parent birds or measured and ringed nestlings before the video-recordings because these processes can affect parental provisioning behaviour (Seress et al. 2017). After ringing the nestlings, we did not check the nest boxes to avoid the risk of premature fledging. Shortly after the expected day of fledging (approx. 22 days after the first nestlings hatched) we emptied the nest boxes and recorded the number of nestlings that died between the ringing and fledging period.

Validating the measuring method (1. question)

Video recordings are commonly used to study the types, amount, and size of food items provided to nestling birds. However, the accuracy and repeatability of estimates of the size of food items from video recordings has not been examined. However, having a repeatable measurement is crucial for ensuring accuracy, reliability, reproducibility, and the ability to compare and analyse data, particularly, if more than one person are involved in the data process. During the measuring process, we took a screenshot of each feeding event when a parent bird held the prey item in front of the nest box's entrance hole (used as size reference, its diameter is always 32 mm). We measured the prey's length and width digitally with the program ImageJ as well as calculated its volume (in mm^3) assuming they had the shape of a cylinder (Slagsvold and Wiebe 2007). We approached the validation of the measurement method in two ways. First, we tested its accuracy, i.e. how the measurements reflect the real size of the prey items. For this, we moulded 40 artificial caterpillars from coloured plasticine to resemble living caterpillars. We measured their size on screenshots and compare these measurements with their real size measured with a caliper. Second, to test whether the measurements of actual prey items from video-recordings were reproducible, we selected 40 prey items from the video-recordings. For testing within-observer reliability, one person measured these items twice, whereas, for testing among-observer reliability, three people measured each item.

Habitat differences in nestling diet (2. question)

According to the food limitation hypothesis, the shortage of high-quality nestling food (caterpillars) in cities is a major factor responsible for the reduced reproductive performance in insectivorous birds. To study this explanation we made a 60-minutes long video-recording per breeding pair in nestling age of 8-12 days (153 nests, first broods). We conducted the study over three breeding seasons (2014-2016) that showed marked between-year differences in both the biomass of canopy-dwelling caterpillars and the great tits' reproductive success (Seress et al. 2018). From the video-recordings for each parental visit, we determined the *prey type* ('caterpillar', 'other arthropod', 'non-arthropod'), measured their length and width from the screenshots as well as calculated their volume (in mm^3). From the prey volume data, we calculated the *average prey volume* for each brood which refers to the volume of food delivered to the nest per feeding event (mm^3). We also calculated the *hourly prey volume* per nestling for each brood, which refers to the total amount of food that one nestling received during the observation. Besides, for each broods, we determined the *number of feeding visits* and calculated *feeding rate* (the number of feeding visits per nestling). Finally, individual *caterpillar volume* (mm^3) was also a separate variable, since earlier studies showed that large-sized caterpillars may play an important role in nestlings development (Schwagmeyer and Mock 2008).

Seasonal differences in nestling diet (3. question)

Those insectivorous birds that have multiple broods within a season generally experience lower reproductive success later in the season. One potential explanation is the food limitation hypothesis i.e. the seasonal decline of high-quality food (caterpillars) is the major driver of the reduced reproductive success observed in second broods compared to first broods. According to our previous results, caterpillar biomass decreases as breeding season progresses, although the decline was less pronounced in cities. Based on these, in this study we examined whether nestling diet and breeding success differ between first and second broods of the same pairs. In this study, we involved individually identified great tit pairs who had successfully raised both their first and second broods during a breeding season (10 forest, 22 urban pairs). We analysed the provisioning behaviour of the parents via 60-minutes long video-recordings that were made in nestling age of 8-12 days. As before, from the video-recordings for each parental visit, we determined the *prey type* ('caterpillar', 'other arthropod', 'non-arthropod'), measured their length and width from the screenshots as well as calculated their volume (in mm^3). From the prey volume data, we calculated the *average prey volume* for each brood which refers to the volume of food delivered to the nest per feeding event (mm^3). For each brood we recorded the *feeding rate* (the number of feeding visits per nestling). Individual *caterpillar volume* (mm^3) was also a separate variable, since earlier studies showed that large-sized caterpillars may play an important role in nestlings development (Schwagmeyer and Mock 2008). The reproductive success of the first and second broods was characterized by three variables: *maximum brood size* (the maximum number of potentially hatched nestlings in a brood), *nestlings' body mass* at ringing age, and *nestling survival* (the proportion of hatched and ringed nestlings).

4. RESULTS IN THESIS POINTS

1. question: I validated a frequently used method for quantifying nestling food from video recordings. I proved experimentally that measuring the length and width of artificial caterpillars on screen provides accurate, unbiased and highly repeatable data of their real size parameters. I showed that the diameter of the nest box's entrance hole can be properly used for size reference purposes. I also justified that accurate measurements can be made by multiple observers if observers are provided with a clear description of the measurement protocol.

2. question: In those two years of the study when markedly lower caterpillar biomass and reproductive success was reported in urban compared to forest habitats during first broods, I found that the quantity of food per nestling provided by the parents did not differ between the habitats. This is the consequence of the result that, although urban parents brought smaller prey items to their nestlings, they fed them relatively more often. Besides, in these two years, urban parents provided more non-arthropod food instead of caterpillars compared to the forest parents. In contrast, in that year when there was only small difference in caterpillar biomass and reproductive success between the habitats, urban parents were able to compensate for the scarcity of caterpillars by provisioning other arthropods and delivering cc. twice as large caterpillars as in the other two years.

3. question: In forest habitats I found no seasonal difference in nestlings' diet, i.e. nestlings received similar composition and amount of food in seasonally first and second broods, and their body mass and survival did not differ between the broods either. Since forest parents reared fewer chicks during their second broods, these results imply that they were able to adjust their brood size to the changing local food availability and rear all hatched nestlings successfully. In contrast, urban great tits tended to bring fewer caterpillars in second compared to their first broods and I observed decreased nestling survival in urban second broods. These results suggest that urban parents are not able to adjust their brood size properly to the changing caterpillar availability in second broods.

Summary: Both field studies supported the food limitation hypothesis, suggesting that the reduced availability of high-quality food (caterpillars) is probably a major driver of the reduced reproductive success observed in first and second broods in the studied cities. However, our results also suggest that sometimes it is possible to catch a better year in the city when urban parents can feed their nestlings with large caterpillars and relatively more non-caterpillar arthropods rather than non-arthropod prey, which may cause detectable increase in urban birds' reproductive success. The results also highlight that long-term studies on urban populations with robust sample sizes are needed to fully understand the implications of among-year variation in environmental conditions.

5. PUBLICATIONS

Publications included in the thesis

1. **Sinkovics**, **C.**, Seress, G., Fábián, V., Sándor, K. & Liker, A. (2018): Obtaining accurate measurements of the size and volume of insects fed to nestlings from video recordings. *Journal of Field Ornithology* 89(2): 165-172; IF: 1.33
2. **Sinkovics**, **C.**, Seress, G., Pipoly, I., Vincze, E. & Liker, A. (2021): Great tits feed their nestlings with more but smaller prey items and fewer caterpillars in cities than in forests. *Scientific Reports* 11: 24161; IF: 4.6
3. **Sinkovics**, **C.**, Seress, G., Pipoly, I., Vincze, E. & Liker, A. (2023): Comparison of nestling food between first and second broods of great tits in urban and forest habitats. *Animal Biodiversity and Conservation 46.2: 199-212;* IF: 1.069

Publications not included in the thesis

1. Pipoly, I., Preiszner, B., Sándor, K., **Sinkovics, C.**, Seress, G., Vincze, E., Bókony, V., Liker, A. 2022. Extreme hot weather has stronger impacts on avian reproduction in forests than in cities. *Frontiers in Ecology and Evolution*, 10:825410; IF: 4.496
2. Sándor, K., Seress, G., **Sinkovics, C**., Péter, Á., Liker, A. 2022. Differences in feather structure between urban and forest great tits: constraint or adaptation? *Journal of Avian Biology*, DOI: 10.1111/jav.02922; IF: 2.248
3. Bukor, B., Seress, G., Pipoly, I., Sándor, K., **Sinkovics, C.**, Vincze, E., Liker, A. 2022 Double-brooding and annual breeding success of Great Tits (Parus major) in urban and forest habitats *Current Zoology*, 68(5), DOI: 10.1093/cz/zoab096; IF: 2.734
4. Vincze, E., Bókony,V., Garamszegi, L. Z., Seress,G., Pipoly,I., **Sinkovics, C.**, Sándor, K., Liker, A. 2021. Consistency and plasticity of risk-taking behaviour toward humans at the nest in urban and forest great tits Parus major. *Animal Behaviour*, 179(18):161-172; IF: 3.041
5. Sándor, K., Liker, A., **Sinkovics, C.**, Péter, Á., Seress, G. 2021. Urban nestlings have reduced number of feathers in Great Tits (Parus major). *IBIS*, 163(4):1369-1378; IF: 2.351
6. Seress, G., Hammer, T., Bókony, V., Vincze, E., Preiszner, B., Pipoly, I., **Sinkovics, C.**, Evans, K. & 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. IF: 6.105

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