DOCTORAL (PHD) DISSERTATION

THE EFFECTS OF URBAN ENVIRONMENT ON REPRODUCTIVE SUCCESS AND PLUMAGE CHARACTERISTICS OF BIRDS

Krisztina Sándor

Doctoral School of Chemistry and Environmental Sciences

Supervisor:

Dr. András Liker

Professor, Behavioural Ecology Research Group

University of Pannonia
Center for Natural Sciences



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INTRODUCTION

Urbanization is a major form of global anthropogenic landscape conversion. Urban animals are constrained by numerous factors including the spatial extent, composition and structure of vegetation, exposure to a range of pollutants (e.g. chemical, noise, heat; Isaksson 2010, Meillère *et al.* 2015), human disturbance, altered microclimate and, for some species, reduced availability of resources including food. These changes could be strong drivers of fast evolutionary responses in cities, making urban habitats an ideal setting to study the adaptability of species to rapid ecological changes.

Food limitation in urban habitats

Due to the powerful landscape transformations, the altered vegetation composition (e.g. high proportion of alien species), and the use of pesticides and herbicides in urban areas, the arthropod communities have dramatically changed (e.g. Vergnes *et al.* 2012, New 2015) in cities. Although insects' responses to urbanization are diverse and taxon-specific, several studies have found that urban environments harbour a strongly reduced amount of insects (Jones & Leather 2012, New 2015, Fenoglio *et al.* 2020), usually characterized by smaller body sizes (Merckx *et*

al. 2018). These changes in insect communities result in a relative scarcity of high-quality food sources (e.g. lepidopteran larvae; Narango *et al.* 2018, Seress *et al.* 2018, 2020, Jarrett *et al.* 2020) for insectivorous animals, like many bird species. The scarcity of urban insects may drastically alter the quantity and quality of food for urban insectivorous animals, suggesting limited availability of high quality food during the most nutritionally demanding life-history stages, like reproduction, nestling development or feather growth of birds.

Urban heat island

Cities are often characterized by higher ambient temperatures and drier microclimate compared to the surrounding non-urbanized areas (so-called urban heat island – UHI; Oke 1982, Arnfield 2003), which is mainly caused by elevated amounts of heat-absorbing and re-radiating surfaces, reduced vegetation cover, air pollutants and anthropogenic heat release (Rizwan *et al.* 2008). Besides the constant warmer microclimate in cities, the UHI may amplify the effects of extreme events caused by climate change, such as heat waves. In such significantly altered microclimatic conditions, along with certain negative effects (e.g. lower nestling survival, smaller body mass; Pipoly *et al.* 2013, Conrey *et al.* 2016), we can assume various adaptive changes as well. A

possible adaptive change could involve changes in the characteristics of the plumage (such as feather structure and number of feathers) that ultimately facilitate passive heat dissipation.

THESIS OBJECTIVES

During my doctoral studies, I focused on two main topics, both of which are integral parts of current research on the effects of urbanization on wild populations. First, in a controlled food manipulation experiment, I studied one of the most fundamental impacts of the urban environment: the effects of food limitation on the reproductive success of birds. Second, I examined the effects of the urban environment on plumage characteristics, in which, in addition to constraints due to food limitation, adaptation to the altered urban microclimate may also play a crucial role.

Specifically, my aim was to answer the following questions:

1. How does the food limitation of the urban environment affect the reproductive success of urban birds?
2. Is there any difference in the structure of contour feathers between urban and forest birds?

3. Is there any difference in the structure of flight feathers between urban and forest birds?
4. Is there any difference in the number of feathers and the density of plumage in the ventral feather tracts between urban and forest birds?

METHODS

As a model organism, we studied the great tits *(Parus major)*, a small insectivorous passerine species common in urban and natural habitats across the Western Palearctic (Gosler & Clement 2007). We carried out these studies in two urban (Veszprém and Balatonfüred) and two forest (Vilma-puszta and Szengtál) nestbox-breeding populations of great tits in Hungary.

Food manipulation experiment

We conducted this study in 2017 at a forest and an urban (Vilma-puszta and Veszprém) site. To test the food limitation hypothesis, we manipulated nestlings' diet in a field experiment, in which great tit broods were allocated to a food supplementation treatment (treatment group) or received no extra food (control group). Treatment broods received supplementary food

(mealworms provided in feeder boxes attached to the nestboxes) on a daily basis when nestlings were 3-15 days old. We adjusted the amount of mealworms according to brood size and nestling age to cover 40-50% of daily food requirements of great tit nestlings (Gibb and Bets 1964, Van Balen 1973, our own unpublished data). Control broods did not receive supplementary food but their nests were also checked daily and we spent a similar amount of time (c. 3-4 minutes) at the nest during each visit to ensure that control and supplemented broods received the same level of human disturbance. When nestlings reached 15-days of age (i.e., just before fledging) we ringed and weighed them (± 0.1 g) and also measured the length of the left tarsus (± 0.1 mm) and right wing (± 1 mm). We also calculated the survival rate for each brood as the proportion of nestlings that survived from day 3 to day 15.

To test the food limitation hypothesis, we analyzed the differences in the following group pairs: (1) forest control vs. urban control (to confirm the effect of habitat on control broods); (2) forest control vs. forest supplemented and (3) urban control vs. urban supplemented (to test for the effects of supplementary food within habitat types); and finally, (4) forest control vs. urban supplemented (to test whether the food-supplementation was sufficient to eliminate or considerably mitigate differences between habitats).

Habitat differences in feather structure

We carried out our study between 2016 and 2018 in two urban and two forest sites. We captured great tits and we plucked 3-5 yellow contour feathers from the upper side of the breast, and also collected the innermost primary from the right wing and the second outermost tail feather from the left side from each individual. Captured birds were ringed with numbered metal rings, and we also determined their sex and age based on their plumage characteristics (Svensson 1992). We differentiated between two age groups (first-year birds and birds after the first year) because these birds grew their feathers under different developmental conditions, which may ultimately affect their feather quality. Then, to examine the structural properties of feathers, we conducted manual measurements on all types of feathers, as well as digital measurements on photos taken with a stereomicroscope. In statistical analyzes, we compared the structural properties of feathers between urban and forest birds, separately for both age categories.

Habitat differences in the number of feathers of nestlings

We carried out our study in April-May 2018 in two urban and two great tit populations. To count the number of feathers, we developed a novel method that is, contrary to the former studies

(e.g. Wetmore 1936, Osváth et al. 2018), non-invasive (i.e., it does not require the plucking of birds' feathers) and can be applied on living specimens.

From egg-laying, we monitored nestboxes at least twice a week to determine the exact hatching date. When the broods reached the age of 6-9 days, we took close-up photos of the sternal region of the nestlings' ventral feather tract. This age range represents an optimal developmental stage for this measurement because feathers have already emerged from the skin within the main feather tracts (pers. obs.) but they are still covered by sheaths – thus, in this stage, feathers do not overlap and can be counted accurately. On the photographs, we determined the borderlines of the sternal feather tract and we counted the number of contour feathers, and also measured the size of the outlined body surface area. Then we calculated the density of contour feathers as feather number divided by the area. To investigate the potential effects of urbanization, we compared the measured variables between urban and forest great tit populations.

THESIS POINTS

Food availability limits avian reproduction in the city: an experimental study on great tits

1. I investigated the effects of the food limitation in urban environment on the reproductive success of urban birds. I showed that the urban nestlings that did not receive supplemental food in a field experiment had significantly smaller body sizes and lower survival rates than non-supplemented nestlings in the forest. However, these habitat differences almost completely disappeared when urban broods received supplementary food: supplementary fed urban nestlings had similar body sizes and survival rates to those of control broods in the forest environment. In contrast, food supplementation in forest broods had small and non-significant effects on these traits. These results provide one of the strongest evidence that food limitation is primarily responsible for the smaller body size and reduced reproductive success of urban birds.

Differences in feather structure between urban and forest great tits: constraint or adaptation?

2. I compared the structural properties of contour feather of urban and forest birds. I found that the urban environment only affected the contour feathers of first year old birds, while I did not find any difference in adults. The urban first year great tits had

contour feathers with lower densities, which ultimately provides a looser plumage structure in these birds. Although it is not entirely clear from the interpretations of previous studies how different densities of feathers affect the thermal insulation, I assume that in the studied urban populations the looser plumage provides better heat dissipation for birds. These changes in contour feathers are probably driven by the adaptation to the warmer climate in cities.

3. I also compared the structural properties of flight (wing and tail) feathers between urban and forest birds. I did not find any habitat differences in adult birds, however, I detected differences in two traits of wing feathers in first year birds. Based on the results of previous studies, these changes may negatively affect the flight performance of first year birds, which may ultimately affect their chances of survival until their subsequent moult. The habitat differences in wing feather structure may be explained by the effects of several environmental constraints, for example the poorer quality of food available to insectivorous birds in the urban environment.

Urban nestlings have reduced number of feathers in great tits

4. I investigated the differences in the number of contour feathers and the density of plumage between urban and forest great tit nestlings at the age of 6-9 days. I found that urban nestlings had significantly fewer feathers and smaller feather tract area (probably implying larger bare body surfaces) than forest ones. This latter finding may indicate an adaptation to the warmer urban microclimate, as bare body surfaces can promote heat dissipation of birds. The fewer contour feathers in urban great tits may also indicate adaptation to urban heat, but can also be the result of nutritional constraints experienced by urban egg-laying females caused by the altered food availability in cities.

PUBLICATIONS

Publications included in the thesis:

1. 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*. *J. Anim. Ecol.* 89: 1570–1580. DOI: https://doi.org/10.1111/1365-2656.13211
2. **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: 1369–1378. DOI: https://doi.org/10.1111/ibi.12948
3. **Sándor, K.,** Seress, G., Sinkovics, Cs., Péter, Á., Liker, A. (2022) Differences in feather structure between urban and forest great tits: constraint or adaptation? *Journal of Avian Biology*. 2022:1-11. DOI: https://doi.org/10.1111/jav.02922

Publications and manuscripts not included in the thesis

1. Seress, G., **Sándor, K.,** Bukor, B., Hubai, K., Bókony, V., Liker, A. (manuscript). Tracking great tits using radio telemetry techniques - investigating territory use and offspring care in urban green areas.
2. **Sándor, K.,** Faragó, K, Skaf, J., Lőrincz, A., Miklósi, Á. (manuscript) Automated bird behaviour analysis on Great tit (Parus major) videos.
3. Pipoly, I., Preiszner, B., **Sándor, K**., Sinkovics, Cs., Vincze, E., Seress, G., 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. DOI: https://doi.org/10.3389/fevo.2022.825410

4. **Sándor, K.,** Könnyű, B. & Miklósi, Á. (2021) Uncertainty in experts' judgments exposes the vulnerability of research reporting anecdotes on animals' cognitive abilities. *Scientific Reports* 11, 16255. DOI: https://doi.org/10.1038/s41598-021-95384-x

5. Seress, G., **Sándor, K.,** Vincze, E., Pipoly, I., Bukor, B., Ágh, N. & Liker, A. (2021) Contrasting effects of the COVID-19 lockdown on urban birds' reproductive success in two cities. *Scientific Reports* 11, 17649. DOI: https://doi.org/10.1038/s41598-021-96858-8

6. Vincze, E. Bókony, V., Garamszegi, L. Z., Seress, G., Pipoly, I., Sinkovics, Cs., **Sándor, K.** & Liker, A. (2021) Consistency and plasticity of risk-taking behaviour towards humans at the nest in urban and forest great tits, *Parus major*. *Animal Behaviour* 179: 161-172. DOI: https://doi.org/10.1016/j.anbehav.2021.06.032

7. Bukor, B., Seress, G., Pipoly, I., **Sándor, K.,** Sinkovics, Cs., Vincze, E., Liker, A. (2021) Double-brooding and annual breeding success of great tits in urban and forest habitats. *Current Zoology*. 68: 517-525. DOI: https://doi.org/10.1093/cz/zoab096

8. **Sándor, K.**, Miklósi, Á. (2020) How to report anecdotal observations? A new approach based on a lesson from "Puffin tool use". *Frontiers in Psychology.* 11:1-5. DOI: https://doi.org/10.3389/fpsyg.2020.555487

9. *Péter, Á., *Seress, G., **Sándor, K**., Klucsik, P. K., Vincze, E., Liker, A. (2020) The effect of artificial light at night on the biomass of caterpillars feeding in urban tree canopies. *Urban Ecosystems,* 23: 1311–1319. DOI: 0.1007/s11252-020-00999-z (* joint first authors)

10. Sinkovics, Cs., Seress, G., Fábián, V., **Sándor, K.**, Liker, A. (2018) Obtaining accurate measurements of the size and volume of insects in nestling diet from video-recordings. *Journal of Field Ornithology* 89: 165-172. DOI: 10.1111/jofo.12248

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