URBANIZATION AND CLIMATE CHANGE: INTERACTIVE EFFECTS ON PHENOLOGY AND REPRODUCTIVE SUCCESS IN NATURAL POPULATIONS

Final report for grant no. K 112838

Reporting period: 01.01.2015 - 31.12.2019

1. Background

The main aim of the project was to investigate the impact of two major recent environmental change, climate warming and urbanization, on reproductive phenology and success of wild animal populations. We successfully completed most of the proposed studies, including all planned fieldwork and the analyses of the resulted data. We had somewhat slower progress with the publication of the results than we anticipated. Therefore we extended the duration of the project until 31 December 2019 by which we were able to publish a significant part of the research and finished several manuscripts. In the final report, we provide brief summaries for the published results, and describe the unpublished studies in more details. Besides these work, we completed several other studies related to the objectives of the grant, which we also summarise in this report.

2. Studies within the main objectives of the grant:

2.1. Methodological studies:

Several kinds of ecological and behavioural data we used in the research were obtained by observing individually marked birds and by standardised video recordings. To assess that these methods can be used reliably for our purposes, we conducted two studies.

First, we analysed the data from an experiment conducted in 2014, in which we tested whether (1) capturing parent great tits during breeding, and (2) the use of small video cameras attached to the nest boxes affect the birds' wariness and the intensity of their parental behaviour. We found that male parents captured and ringed become significantly more wary and bring less food to the nestling than control males for several days after capture, whereas no effects were detected in females. Based on this result, we considered ringing status of parents in other studies conducted in the project. The presence of the video camera does not influence the parents' behaviour, since birds that were familiarized with the camera for 2-3 weeks did not differed form control birds that were not allowed to habituate to the camera (***Seress et al. 2017. Journal of Field Ornithology 88: 299-312***).

Second, we tested the suitability of video images for identifying and measuring prey items brought by the parent birds to feed their offspring. We showed that type and size can be determined for 57% of prey items, and that prey sizes measured from video recordings are both accurate and highly repeatable (***Sinkovics et al. 2018. Journal of Field Ornithology 89: 165-172***).

2.2. Food availability and seasonality, and reproductive success of urban birds

To test whether urbanization impacts on food sources of wild urban birds, we studied the seasonal changes of the biomass of tree dwelling caterpillars (one of the main food sources of several arboreal birds) in two urban and two forest study sites over four years, by analysing more than 4500 caterpillar frass samples. Despite a trend of earlier leaf emergence in urban sites, there is no evidence for an earlier average peak in caterpillar abundance. Thus the earlier breeding of urban bird populations is not associated with an earlier peak in

caterpillar availability. However, seasonal dynamics of caterpillar biomass exhibited striking habitat differences with a single clear peak in forests, and several much smaller peaks in urban sites. Caterpillar biomass was higher in forests than urban areas across the entire sampling period, and between 8.5 and 24 times higher during the chick-rearing period. Urban great tits laid smaller clutches, experienced more frequent nestling mortality from starvation, reared fewer offspring to fledging age, and their fledglings had lower body mass. These results indicates that food limitation is responsible for lower avian reproductive success in cities, which is driven by reduced availability of the preferred nestling diet rather than phenological shifts in the timing of peak food availability (***Seress et al. 2018. Ecological Applications 28: 1143-1156***).

To investigate further that reduced avian reproductive success in cities is driven by low insect availability during the breeding season, we conducted an experiment that provided supplementary insect food (nutritionally enhanced mealworms supplied daily to meet 40-50% of each supplemented brood's food requirements) to great tit nestlings in urban and forest habitats. As predicted by the food limitation hypothesis, we found that urban supplemented nestlings had larger body size and survival rates than those in urban control broods, and crucially urban supplemented broods had similar body size and survival rates to nestlings in forest control broods. These results provide robust experimental support for the strong negative effects of food limitation during the nestling rearing period on urban birds' breeding success. Furthermore, the fact that supplementary food almost completely eliminated habitat differences in survival rate and nestling body size suggest that urban stressors other than food shortage contributed relatively little to the reduced avian breeding success. Finally, given the impacts of the amount of supplementary food that we provided and taking clutch size differences into account, our results suggest that urban insect populations in our study system would need to be increased by a factor of at least 2.5 for urban and forest great tits to have similar reproductive success (***Seress et al., Journal of Animal Ecology, in revision***; preprint is available from the REAL repository).

We also analysed our long-term dataset on caterpillar biomass and the birds' breeding to investigate whether urbanization influence the synchrony between the timing of breeding and food peak, and how synchrony affects breeding success. We found that the variance in synchrony differed significantly between study sites (Figure 1), indicating a generally lower synchrony (i.e. higher variance) of urban broods with the seasonal caterpillar peak.

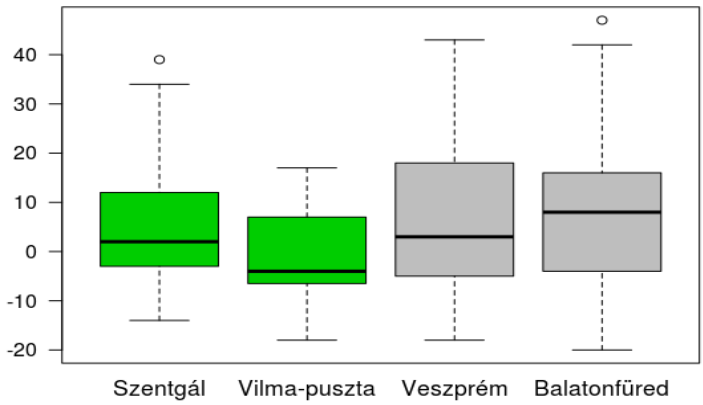

Figure 1. *Synchrony (in days) between broods and the annual food peaks in the four study populations. 0 day synchrony means that nestlings in a brood was 10 days old (nestling age with maximum food demand in great tits) on the day of annual peak caterpillar biomass of the site.*

We also tested if the degree of synchrony with the food peak affected the broods' reproductive output. We found that fledging success (the proportion of nestling that reached fledging age) was affected by both synchrony and study site. However, the effect of synchrony on fledging success was significant only at the two forest sites, whereas no such effect was detectable at the two urban sites. These results suggest that habitat urbanization increases the mismatch between the timing of breeding and maximum food availability, and that breeding success in urban sites is decoupled from the peak of caterpillar biomass, for example because caterpillars provide a less significant portion of nestling diet in urban sites (***G. Seress, B. Bukor and A. Liker, unpublished results***).

To investigate the effects reduced urban caterpillar availability on nestling diet and parental behaviour, we videotaped the provisioning behaviour of great tit parents at 153 broods in two urban and two forest sites over three years. We recorded the number of feeding visits by the parents, categorized the type of the delivered prey items (caterpillars, other arthropods, non-arthropod food) and estimated their volume. We found that the proportion of caterpillars was only 65% in urban habitats, whereas 88% in the forests (Figure 3). We detected annual differences in the parents' feeding activity and the amount of nestling food. In two years when we observed reduced reproductive success in urban areas, we found that urban parents delivered smaller prey items per feeding visit than the pairs breeding in forests. However, parents fed their nestlings more frequently in urban than in forest sites, resulting in similar total amount (volume) of food received by nestlings in the two habitats. In contrast, in the third year when the difference in the reproductive success between the habitats was small, we did not observe habitat differences either in the feeding rate or in the average volume of the delivered prey items per feeding visits. In this latter year urban nestlings received larger caterpillars than in the other two years, and the volume of the caterpillars received by nestlings did not differ between habitats. These results suggest that by reducing clutch size and increasing the feeding activity urban parents are able to provide the same amount of food as parents breeding in forest habitats with much higher caterpillar abundance. However, food quality may be worse in the cities (probably due to less caterpillars in the nestling diet) which constraint the development of urban nestlings in most years **(*Sinkovics et al. manuscript in preparation*)**.

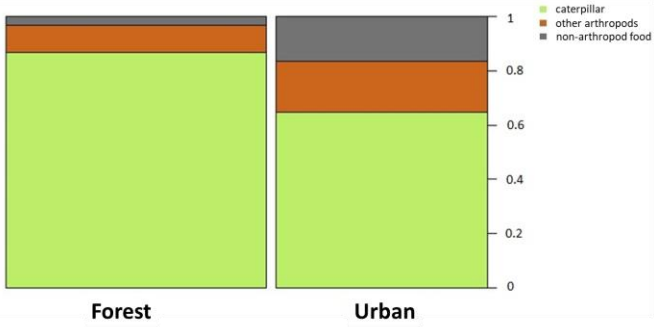

Figure 2. *The composition of nestling diet in forest and urban broods of great tits. Bars show the proportion of prey brought by parents that were categorised as caterpillar, other arthropod, and non-arthropod food items (n= 2316 prey items).*

In follow up studies, we also showed (1) that urban caterpillar biomass is not related to the intensity of artificial night light (light pollution) measured around the sampled trees (***Péter et al. Urban Ecosystems, in revision***; preprint is available from the REAL repository). (2) We showed that most urban caterpillar belongs to lepidopteran species that also occur in the nearby forest sites, and the species found in cities are present as caterpillars for longer

periods of the year then species which only occur in forest **(*Bubla 2018. BSc thesis*)**. (3) We measured the carotenoid content in individual caterpillars and found caterpillars from oak (Q. cerris) trees were richer in carotenoid than caterpillars from ash (F. ornus), beech (F. sylvatica) or hornbeam (C. betulus) trees **(*Ayele Woldemanuel 2018. MSc thesis*)**.

2.3. The effects of extreme weather on reproduction of urban and non-urban birds:

Extreme weather events are rare, but can have high impact on both human societies and biological systems. As the frequency of extreme events are increasing with current climate change, it is important to understand its effects on fitness of individuals and on long-term viability of populations. Using monitoring data on reproductive success of more than 700 great tit nests and hourly meteorological records from the study sites, we investigated the effects of high ambient temperatures on the birds' breeding success in two urban and two natural forest populations during six years. We found that the number of hot days was higher in urban than in forest sites and had habitat-specific effects on nestlings during their development period (from hatching to 15-days of age). Average body mass of broods decreased with increasing number of hot days in both forest populations and one city population. However, the negative effect of hot days on chick mass was significantly stronger in forest than in urban populations (Figure 2), suggesting that forest populations are more vulnerable to extreme hot weather conditions. Unlike the other study populations, average chick mass increased with the number of hot days in the hottest urban study site, suggesting adaptation in heat tolerance in this population. Tarsus length of chicks and their survival until fledging was not influenced significantly by hot weather.

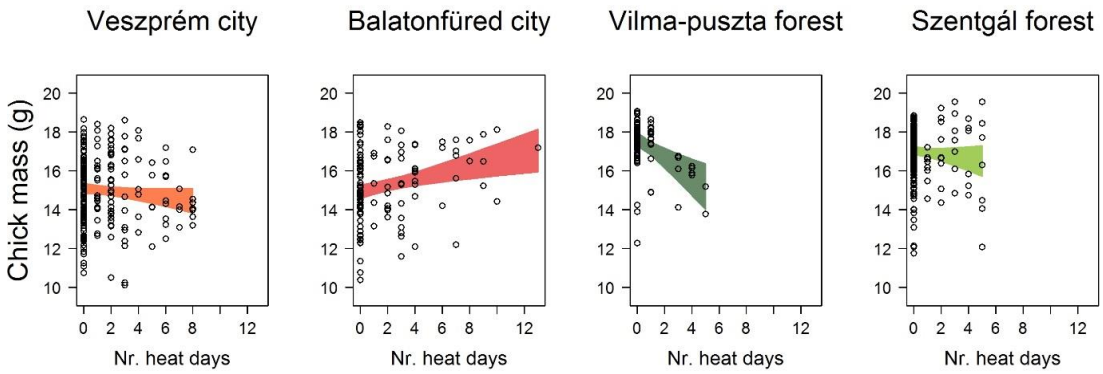

Figure 3. *Relationship between average body mass and number of hot days in urban and forest study sites. Coloured stripes show the 95% confidence band of the slope of relationship. The slope is negative for Veszprém, Vilma-puszta and Szentgál, and positive for Balatonfüred.*

Hot weather conditions may affect the reproductive output of birds in at least two ways: indirectly through food availability and directly through nestling physiology. As tarsus length and survival of chicks were not affected by exposure to hot days in our study, we suggest that the negative effect of hot days on body mass may emerge more likely from the direct physiological effects of heat. These results are one of the first demonstrations that the effects of extreme weather events can differ between wild populations living in differently urbanized environments. The results are reported in a recent PhD dissertation (***Pipoly 2020***) and in a manuscript (***Pipoly et al. unpublished manuscript***; preprint is available from the bioRxiv repository).

2.4. Habitat use by urban birds: a pilot radio telemetry study

We completed the development of a system and protocol for automated radio telemetry for tracking small urban birds. First, we carried out a short experiment using captive great tits in which we tested the effects of radio transmitters attached to the birds on their behaviour.

The results suggest that the application of <1 g transmitters could decrease the activity of birds during the first 1-3 days, but thereafter they behaviour recovers and does not differ from control birds (***T. Hammer et al. unpublised results***). Then we set up an automated tracking system, which includes 6 fix-position receiver towers, a central receiver unit and a computer running a software specifically designed to integrate data of the receivers. In addition, we developed a method for spatial calibrations of the received signal patterns of the studied area, which allows more precise localisation of the tracked birds. We run several tracking trials that showed that all components of the system work properly and can collect thousands of localizations during 3-5 days of tracking and produce high quality maps of the area visited by the birds (Figure 4; ***A. Liker, E. Vincze and R. Wohlfart unpublished data***).

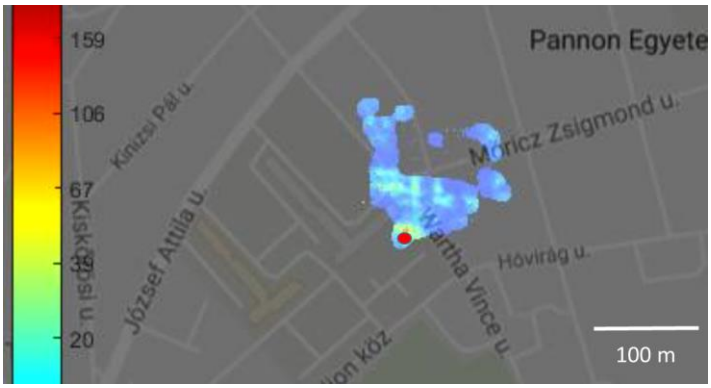

Figure 4. *Map showing the area used by a great tit for collecting food for nestlings. The bright colours highlight the areas visited by the bird during a few hours of tracking. Different colours correspond to different frequency of localizations at specific points, the red dot marks the site of the bird's nest box (visualization produced by R. Wohlfart, BME Budapest).*

3. Studies closely related to project:

We completed several other studies during the reporting period that focused on the ecology and behaviour of urban bird populations:

3.1. Behavioral flexibility:

We published the results of an earlier study in which we showed that urban birds habituate to human disturbance faster than rural birds (***Vincze et al. 2016. Behavioral Ecology 27: 1304-1313***)

We published a paper from an earlier experiment in which we report that great tits with better problem-solving ability have higher reproductive success, both in urban and forest populations (***Preiszner et al. 2017. Animal Cognition 20: 53–63***).

We also showed that female great tits that are better at solving experimental foraging tasks have more extra-pair offspring than the less successful females (***Bókony et al. 2017. Behavioral Ecology 28: 579-588***).

3.2. Reproductive strategies:

We compared the frequencies of extra-pair offspring between two urban and two forest populations of great tits in three years, and found that urban broods contained extra-pair offspring more frequently (48.9%) than broods in natural forests (24.2%) (***Pipoly et al. 2019. Frontiers in Ecology and Evolution, 7: 229***).

We determined the sex of nestlings in 126 complete broods from four years, and found that brood sex ratio did not differ significantly between urban and forest habitats either at egg-laying or near fledging (***Ágh et al. Biologia Futura, in revision;*** preprint is available from the bioRxiv repository).

3.3. Predation risk:

Using meta-analytic methods we showed that the survival rate of artificial nests tends to decrease with increasing urbanization, indicating higher predation of experimental nests in more urbanized study sites. In contrast, the survival of natural nests tended to increase with urbanization levels (***Vincze et al. 2017. Frontiers in Ecology and Evolution 5: 29***).

Using experimental presentations of a predator (sparrowhawk) and human subjects to wild great tits, we showed that urban birds behave more boldly against both stimuli than forest birds. However, there is no correlation between the two risk-taking responses, suggesting that the responses are predator-specific. This also implies that a general level of fear of predators cannot be assessed from the birds' responses to humans (which is often assumed in urban ecology studies) (***Vincze et al. 2019. Ethology, 125: 686–701***).

4. Studies in the broader research field of the project:

Besides the above studies, our research group published further papers during the reporting period that focus on evolutionary ecology of animal populations with feedbacks to the project's objectives. We report here those studies in which the project participant(s) played a dominant roles (i.e. was either leading or senior (last) author).

We showed in birds that parental sex roles are not related to the gametic investment of the sexes, but are associated with sexual selection and the social environment as measured by the adult sex ratio of the populations (***Liker et al. 2015. Evolution 69: 2799–3024***).

Using phylogenetic comparative approach, we discovered that tetrapod species with XY sex determination system have more female-skewed adult sex ratios than species that have ZW sex determination system (***Pipoly et al. 2015. Nature 527: 91–94***).

In a comparative study, using the largest sex-specific dataset on dispersal distances in birds, we showed that sex differences in dispersal is related to adult sex ratio, but is not associated with different aspects of sexual selection and parental care (***Végvári et al. 2018. Ecology and Evolution 13: 6483-6491***).

5. Other outputs of the project:

We published two papers to disseminate the results of our research (***Liker 2015 Magyar Tudomány, Ágh & Seress 2019. Természetbúvár***). From the results of research connected to the project, 6 BSc and MSc theses and 2 PhD dissertations were produced. Our research group initiated and organized the first urban ecology conference in Hungary (1st Urban Ecology Conference, 19-20. October 2019, Veszprém).

6. References:

6.1. Published papers:

Ágh N., Seress, G. 2019. Az urbanizáció és a széncinegék: Fiókanevelés az erdőben és a nagyvárosban. Természetbúvár 74: 46-48.

Bókony V, Pipoly I, Szabó K, Preiszner B, Vincze E, Papp S, Seress G, Hammer T & Liker A. 2017. Innovative females are more promiscuous in great tits (Parus major). Behavioral Ecology 28: 579-588.

Liker, A. 2015. Az éghajlatváltozás és az urbanizáció együttes ökológiai hatásai. Magyar Tudomány 176: 546-552.

Liker, A., Freckleton, R.P., Remeš, V. & Székely, T. 2015. Sex differences in parental care: gametic investment, sexual selection and social environment. Evolution 69: 2799–3024.

Preiszner, B., Papp, S., Pipoly, I., Seress, G., Vincze, E., Liker, A. & Bókony, V. 2017. Problem-solving performance and reproductive success of great tits in urban and forest habitats. Animal Cognition 20: 53–63.

Pipoly, I., Bókony, V., Kirkpatrick, M., Donald, P. F. Székely, T. & Liker, A. 2015. The genetic sex determination system predicts the adult sex ratio in tetrapods. Nature 527: 91–94.

Pipoly, I., Szabó, K., Bókony, V., Hammer, T., Papp, S., Preiszner, B., Seress, G., Vincze, E., Schroeder, J., Liker, A. 2019. Higher frequency of extra-pair offspring in urban than forest broods of great tits (Parus major). Frontiers in Ecology and Evolution 7: 229

Seress G., Vincze E., Pipoly I., Hammer T., Papp S., Preiszner B., Bókony V. & Liker A. 2017. Effects of capture and video-recording on the behavior and breeding success of Great Tits in urban and forest habitats. Journal of Field Ornithology 88: 299-312.

Seress G, Hammer T, Bókony V, Vincze E, Preiszner B, Papp S, Pipoly I, Sinkovics C, Evans KL & Liker A. 2018. Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. Ecological Applications 28: 1143-1156.

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: 165-172.

Végvári Z, Katona G, Vági B, Freckleton R, Gaillard J-M, Székely T, Liker A. 2018. Sex-biased breeding dispersal is predicted by social environment in birds. Ecology and Evolution 13: 6483-6491.

Vincze, E., Papp, S., Preiszner, B., Seress, G., Bókony, V. & Liker, A. 2016. Habituation to human disturbance is faster in urban than rural house sparrows. Behavioral Ecology 27: 1304-1313.

Vincze, E., Seress, G., Lagisz, M., Nakagawa, S., Dingemanse N. J. & Sprau, P. 2017. Does urbanization affect predation of bird nests? A meta-analysis. Frontiers in Ecology and Evolution 5: 29.

Vincze E, Pipoly I, Seress G, Preiszner B, Papp P, Németh B & Liker A. Bókony V, 2019. Great tits take greater risk toward humans and sparrowhawks in urban habitats than in forests. Ethology, 125: 686–701.

6.2. Manuscripts:

Ágh, N., Pipoly, I., Szabó, K., Vincze, E., Bókony, V., Seress, G., Liker, A. Does offspring sex ratio differ between urban and forest populations of great tits (Parus major)? Biologia Futura, in revision (preprint available from the bioRxiv repository).

Péter Á., Sándor K., Seress G., Vincze E., Klucsik K.P., Liker A. The effect of artificial light at night on the biomass of caterpillars feeding in urban tree canopies. Urban Ecosystems, in revison (preprint available from the REAL repository).

Pipoly I., Preiszner B., Sándor K., Sinkovics C., Seress G., Vincze E., Bókony V., Liker A. Effects of extreme hot weather on the reproductive output of great tits (Parus major, L.) in urban and natural habitats. Unpublished manuscript (preprint available from the bioRxiv repository).

Seress G, Sándor K, Evans KL, Liker A. Food availability limits avian reproduction in the city: an experimental study on great tits (Parus major). Journal of Animal Ecology, in revision (preprint available from the REAL repository).

Sinkovics C, Pipoly I, Vincze E, Seress G, Evans KL, Liker A. Effects of urbanization on nestling diet and reproductive success in great tits (Parus major). Manuscript in preparation.

6.3. PhD disserations:

Pipoly I. 2020. Environmental and genetic predictors of reproductive success and sex ratios in vertebrates. PhD dissertation, Doctoral School of Chemistry and Environmental Sciences, University of Pannonia.

Vincze E. 2018. Behavioral responses to humans and predators in urban and non-urban birds. PhD dissertation, Doctoral School of Chemistry and Environmental Sciences, University of Pannonia.

6.4. BSc and MSc theses

Bukor B. 2017. Erdei és városi széncinege (Parus major) populációk éven belüli és évek közötti újrafészkeléseinek gyakoriságának vizsgálata. BSc szakdolgozat, Állatorvostudományi Egyetem, Biológiai Intézet, Ökológia Tanszék, Budapest.

Völgyi N. 2017. Mesterséges kiegészítő táplálék kifejlesztése széncinegék számára, és tesztelése laboratóriumi és szabadon fészkelő madarakkal. BSc szakdolgozat, Pannon Egyetem, Limnológia Tanszék, Veszprém.

Ayele Woldemanuel G. 2018. Comparing the carotenoid content of caterpillars between an oak and beech forest. MSc thesis, University of Pannonia.

Bubla, P. 2018. Erdei és városi fán élő hernyópopulációk összehasonlítása. BSc szakdolgozat, Állatorvostudományi Egyetem, Biológiai Intézet.

Fábián, V. 2018. Ivari különbségek a széncinegék (Parus major) utódgondozó viselkedésében természetes és urbanizált környezetben. MSc szakdolgozat, Pannon Egyetem, Veszprém.

Bukor B. 2019. Széncinegék (Parus major) túlélésének vizsgálata különböző fészkelő helyeken. MSc szakdolgozat, Állatorvostudományi Egyetem, Biológiai Intézet, Ökológia Tanszék, Budapest.