Life-history strategies and juvenile environment in birds

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Final report

Individuals apply different strategies during their life, which strategies have crucial effect on their fitness. The reason of using a strategy can be genetic, but it can be considerably influenced by the environment the individual experience during its life. Early environmental conditions can be particularly important. As the environment changes with time, long-term data help us to explore patterns of life-history strategies, their reasons and consequences.
The major goal of this project was to investigate the life-history strategies of collared flycatcher (*Ficedula albicollis*) with special regard to the effects of juvenile environment. These birds have bred in nestbox plots in Pilis-Visegrádi Mountains for decades, thus a more than 30-year long dataset is available for studying certain problems.

Field work
All over the three years during the breeding season of collared flycatchers (April-June) I collected breeding and morphology data for my further work with the Behavioural Ecology Group of the Eötvös Loránd University. At present, there are approximately 650 nestboxes at the study site. They were checked multiple times a week during the whole nesting period, so breeding attempts were followed from nest building to fledging. We were intent on capturing all parents when feeding young. All nestlings and captured adults were ringed, and the latter ones were measured too. Caterpillar frass was also collected during the breeding season. There were about 200 nestboxes of which coordinates were not known or had badly recorded. I made up the shortage using a GPS.

Natal dispersal
The place of first breeding is crucial for young birds. The decision to settle down plays an important role in determination of the number and the success of breeding attempts, i.e. in fitness. An important question in birds is that in which area they settle, and how far their breeding site is from their birth place, additionally, in many cases, individuals do not disperse too far from their first breeding site. To study this problem, I had to collect data of birds that had been ringed as a nestling, and then were recaptured as a one-year-old breeder (recruit) for which a 36-year database was employed (partly preparing notes written in the field). There are several individuals, which hatched in our study plots, but are observed to breed first there only at the age of two or three years. These individuals could not be taken into account in this study as we could not be sure about that they had not bred elsewhere previously. In each of the 1042 relevant bird I calculated natal dispersal distances. Natal dispersal was defined as the distance between natal nestbox of the given individual and that in which it bred for the first time. So, another important task was to determine the position of each nestbox since 1982 (the first year after they were placed) for computing dispersal distances. This meant about 2300 positions of 1368 nestboxes. It was quite easy for the last fifteen years as we had the GPS

coordinates of all of them, but was much more difficult for plots that had abolished or moved before 2006. In approximately 1000 cases, positions had to be estimated on the basis of maps (occasionally drawn by hand), which could be checked with the help of Google Earth. Certainly, dispersal distances were more inaccurate when these nestboxes were used, but they were correct enough to draw conclusions from the results.

Mean natal dispersal distance of collared flycatchers was 805 ± 696 (SD) m and almost 70 percent of individuals bred within 1000 m from their birth place. Female chicks moved farther than males. Neither the number of fledglings in the nest, nor the amount of food available during the breeding season affected dispersal distance. It was not influenced by the body size of the mother or by the size of secondary sexual characters: forehead patch size of the father and wing patch size of both parents either. However, chicks of yearling males settled down nearer to their birth place than those of older males, and recruits of smaller males also tended to choose a nestbox closer. We plan one manuscript presenting these results.

Dispersal and novel environment

Behaviour in a novel environment could have great importance for fitness, as many animals frequently encounter unfamiliar environments during their life. The successful exploration of novel environments may make available new sources of food, mates, refuges, but it may also incur some costs due to increased risk of predation or parasitism. Behaviour in novel environment reflects general activity, but may also reflect risk-taking. Adaptive behavioural strategies in novel environment may have particular importance in migratory species, because they are frequently exposed to such unknown environments during migration stopovers and also when arriving to the breeding or wintering grounds. Our aim in this study was to characterize behaviours measured in an artificial novel environment and assess the biological relevance of them in the collared flycatcher (*Ficedula albicollis*). We measured the repeatability and the association of multiple behavioural traits, as well as their relationship with dispersal (that reflects exploration in the wild). We assayed the behaviour of the birds in an aviary built in the study area and covered with net. Within the enclosure, we provided three perching trees. In males, behavioural traits in the novel environment had generally low repeatability between years, higher repeatability between the courtship and the chick-feeding period, and high and significant repeatability within a day. In females, the repeatability of these traits was low between years (we could investigate only this interval). Males tended to perch on one of the trees sooner than females. Birds with short perching latency were more likely residents and bred closer to their breeding nestbox in the previous year (Figure 1), which may suggest that latency to perch is connected to dispersal in the wild. The results indicated that a component of behaviour of the collared flycatcher assessed in an unnatural spatial enclosure represents an ecologically relevant trait. A manuscript was submitted to Ethology (Jablonszky et al. 2019).

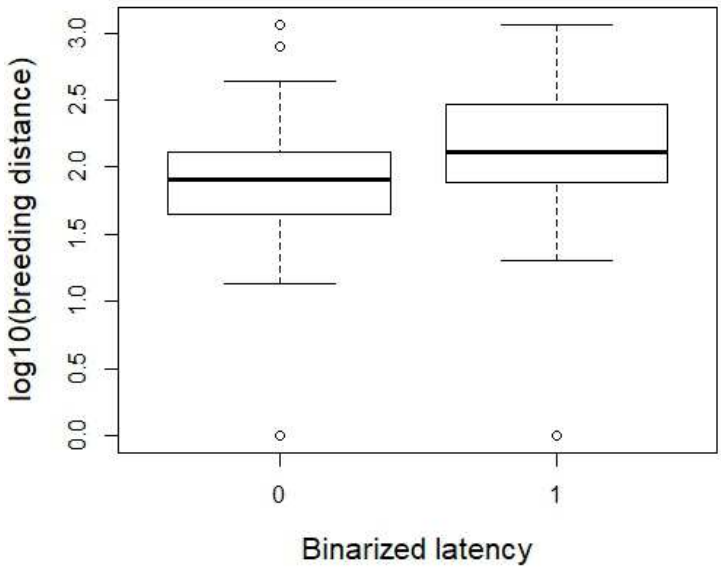
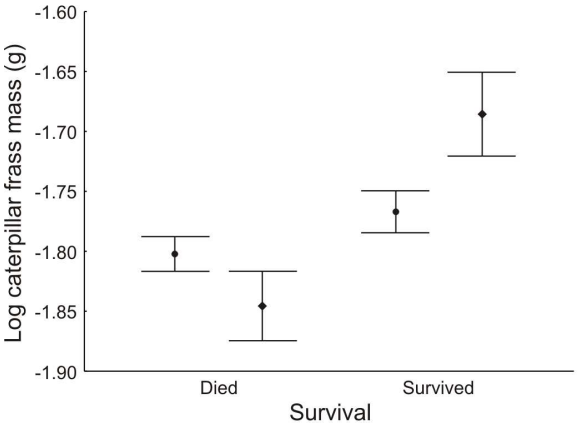


Fig. 1 Relationship between binarized latency to perch (0 – short, 1 – long) and $\log_{10}$ transformed breeding distance (m)

Survival

Survival is one of the main components of fitness. Using an 18-year dataset I studied the relationship between the survival of collared flycatchers and food availability on the breeding ground as well as characteristics of their mate. Only 1-3 year-old individuals were considered to eliminate the effect of senescence. Survival of both sexes was positively associated with food availability in the current year (Figure 2) estimated by the availability of lepidopteran larvae, an important component of the nestling diet of collared flycatchers, estimated on the basis of caterpillar frass mass. In contrast, there was a negative relationship between the survival of males and their age and the size of their forehead patch, respectively. Relationship between the survival of females and the forehead patch size of their mates depended on female body size (Figure 3). Small females paired with a large-patched male survived with lower probability than those paired with a small-patched male, but survival of large females only slightly declined with the increasing forehead patch of their mate. It would be worth investigating the reasons of these relationships later on.



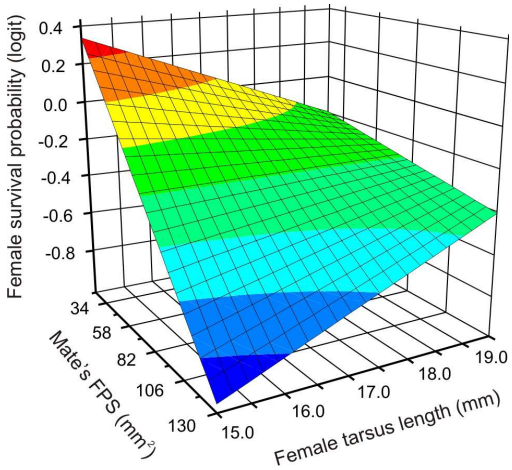


Fig. 2 (left) The relationship between survival of collared flycatchers and the amount of caterpillar frass mass measured on the study plot (mean ± SE). Caterpillar frass mass was log transformed. Females are denoted by circles and males by squares

Fig. 3 (right) Interaction between female body size and mate's forehead patch size on female survival. Survival values are logit transformed. FPS = forehead patch size

Survival can be related to previous reproductive performance. There can be a negative association between them when individuals allocating a higher amount of energy into reproduction have lower survival probability. But a positive relationship can also be detected if there are phenotypic differences in resource acquisition and some individuals allocate greater amounts of resources to several life-history traits while others allocate little. I took the number of eggs, hatching success (hatchling number/clutch size) and fledging success (fledgling number/hatchling number) as reproductive performance, respectively. Among them fledging success of females showed a positive association with survival. However, its effect disappeared when only nests with at least one fledged nestling were taken into account. This suggests that differences in survival were mainly derived from differences between successful and absolutely unsuccessful females. The difference between the survival of individuals with high and low fledging success was more expressed when food availability was high. Females' age and tarsus length was positively related to clutch size and negatively to fledging success, while male age was positively related to fledging success. These results and those mentioned in the previous paragraph were presented in EOU 2017 conference (Turku, Finland) and a manuscript was submitted to Behavioral Ecology and Sociobiology (Herényi et al. 2019).

The survival of birds may be related to their risk-taking and territorial behaviour, thus we also investigated these two characteristics. In the courtship period we conducted behavioural tests on established males. We put out a live, conspecific decoy male in a small cage within 2 m from the focal nestbox. Territorial aggression behaviour was measured assessing the latency of the first attack. It was defined as the time that elapsed between the moments when the resident male detected and first attempted to attack the decoy (specifically, touched its cage from any side). Risk-taking behaviour was estimated by the distance between the decoy male's cage and the last position of the observer approaching the resident male at which the latter did not continue its territorial behaviour. We showed that the relationship between aggression and survival was depended on the age of the male (Figure 4). Among older individuals the less aggressive males had a significantly higher chance to be recaptured in the

next year. While among one-year-old individuals the more aggressive males returned better. Males that took more risk, that is, let the observer closer, had more chicks and their chance to survive to the next year was lower. These results were published in two papers (Jablonszky et al. 2018, Szász et al. 2019).

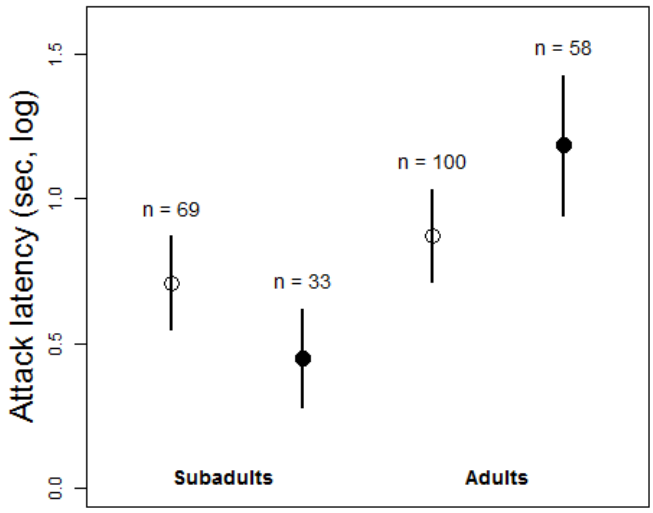


Fig.4 Return of subadult and adult male collared flycatchers in the next year according to the level of their aggression. Open circles and filled circles represent not returned and returned males, respectively. Attack latency values were log10(x+1)-transformed. Means and 95 % confidence intervals are shown

Migration routes and wintering sites

Whereas the migratory routes are relatively well-known in its sibling species, the pied flycatcher (*Ficedula hypoleuca*), we have no or little information about the migration and wintering of collared flycatchers, as there are only very few recapture events from Africa or from the Mediterranean region. In collaboration with the University of Nyíregyháza, after in a Transylvanian cooperation we tried to identify migration and wintering areas of these birds using the above dataset extended with data of 7 years. The determination of wintering area was carried out with independent methods using NDVI (Normalized Difference Vegetation Index) data. NDVI is based on satellite images indicating the condition of rainfall-dependent vegetation in space and time. Comparing survival data and different breeding parameters with vegetational changes in Africa can result in getting the potential areas where flycatchers spend the wintering period. Survival probabilities of flycatchers were determined separately for males and females using the MARK program. We found that in females the probability to survive correlated with that of males. Lots of analyses were performed comparing survival of both sexes and breeding parameters with African vegetation changes in winter and migration periods (between September and April). Preliminary results showed too many areas in Africa, mainly in the Sahel region and in East-Africa, which could be the potential wintering area or a stopover site of our collared flycatchers. Reducing these areas can be performed by refining the survival models. Further investigations are needed in this part of the research.

Breeding phenology and reproductive success

Breeding phenology (arrival at the breeding site, the onset of breeding…), reproductive success and survival may be equally affected by global and local weather conditions and populations may be under selection to respond climatic changes. Because of this, shifting phenology through time might be an indicator of the response of ecosystem dynamics to global warming including advancing spring. Temporal changes in teleconnections (linkages between climate anomalies occurring in widely separated geographical regions) reflect climatic conditions over large areas. They are therefore often considered to be capable of predicting and explaining ecological changes beside local-scale climatic indices. We examined the long-term trends in breeding phenology and reproductive success on birds in the Carpathian Basin, as well as the timing of the availability of their food. We also looked for correlations with local weather patterns (temperature and precipitation) and large-scale climatic variation. We included two other model species: great tit (*Parus major*) and blue tit (*Cyanistes caeruleus*) in the analyses. The amount of their main food type (caterpillars) increases first during the spring, reaches a peak, then declines to a lower level.

In both species, laying date (the date of laying the first egg) was negatively related to February-March Arctic Oscillation (AO) index and also to temperature in January-March (Figure 5), that is, birds laid their first egg earlier when AO index or temperature was higher. However, it did not associate with North Atlantic Oscillation (NAO), East Atlantic Pattern or El Niño-Southern Oscillation. These findings highlight the importance of using 'uncommon' teleconnections and support that the two indices, NAO and AO may correlate with biological processes in a different way. Neither the weather or climatic variables, nor breeding density showed significant relationships with clutch size.

Caterpillar peak was negatively related to December-January temperature and markedly shifted towards earlier dates with year (Figure 6d). The two tit species answered differently to this phenomenon. Laying date in great tits was slightly negatively related to year, but that of blue tits did not advance. Laying date relative to caterpillar peak did not change in great tits, while in blue tits the length of this interval reduced at the beginning and the end of the study period (1987-2015) (Figure 6c). The laying date difference between the two species decreased markedly (Figure 6a). On the other hand, great tit clutch exhibited very little change, in contrast to blue tit clutch size, which showed a minimum in the middle of the study period (Figure 6b). The results are just before publishing in a paper (Laczi et al. 2019 in press).

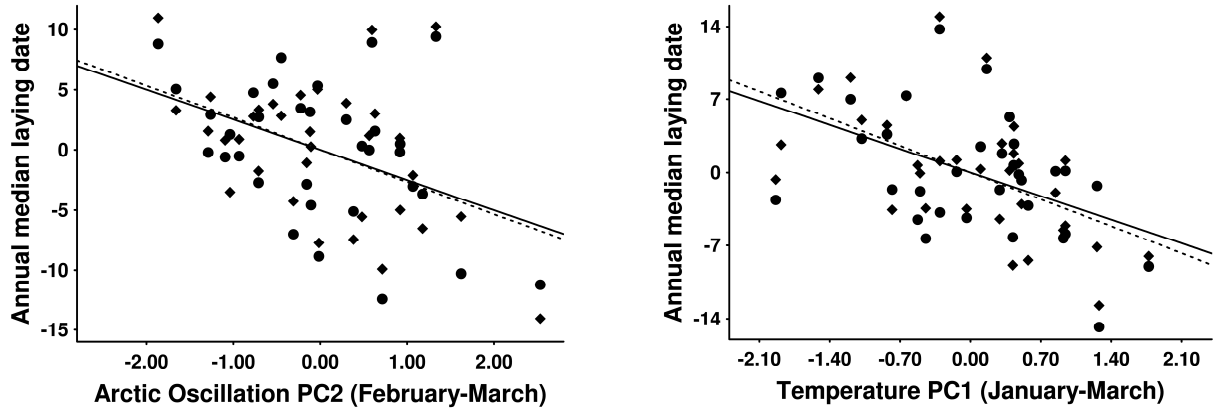


Fig. 5 Relationship of great tit and blue tit laying date with the Arctic Oscillation (left) and with temperature conditions between January and March (right) in the study area. Circles, continuous line: great tit; diamonds, dashed line: blue tit

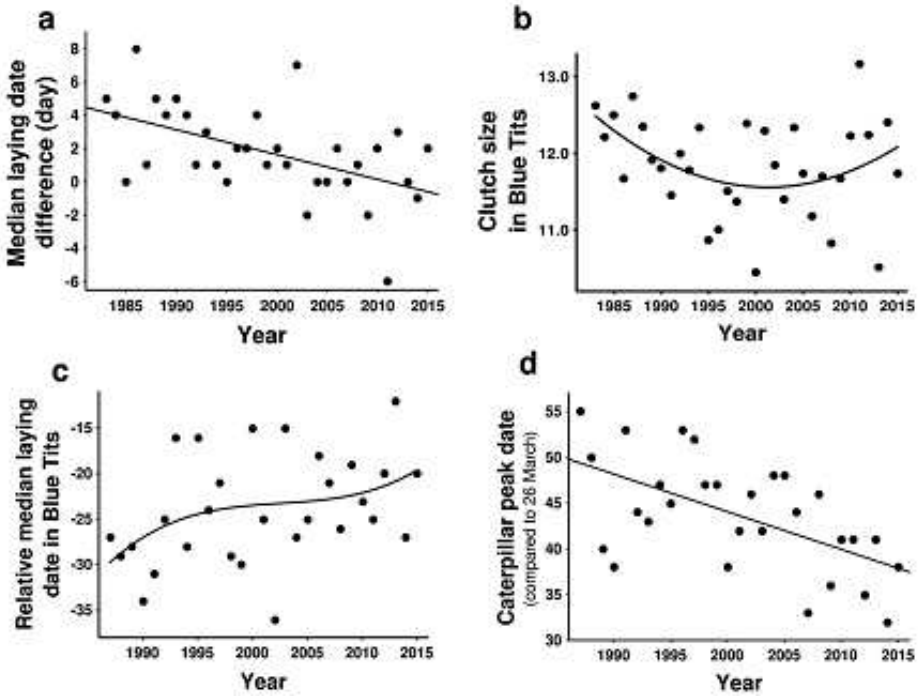


Fig. 6 Yearly trends in the breeding variables of the great tit and the blue tit (a-c) and in the caterpillar peak date in the study area (d). Relative median laying date refers to median of laying date deviations from the caterpillar peak date. Median laying date difference refers to annual laying date difference between species (great tit minus blue tit)

Although such analyses have not been performed in flycatchers so far, we showed that males that started to breed earlier fledged more offspring. Also, timing had a significant role in another estimate of reproductive performance: males that arrive earlier had a higher chance to establish social pair-bond. Arrival date positively correlated with laying date, but among successfully paired males, the later the male arrived, the shorter the time interval between arrival date and laying date was. These results were published in a paper (Szász et al. 2019).

Summary and outlook

Altogether the funded project was successful. Although I could not study all planned questions (like those of the age at first reproduction), in other parts of the research (e.g. that of survival of collared flycatchers) we extended our knowledge more than previously expected. Hence, we gained much information about hole-breeding passerines: their dispersal, survival effects of their behaviour, food supply or characteristics of their mate. While results of simultaneously investigating the timing of breeding, changes in the amount of food and that of climatic conditions shed light on that climate change has a substantial effect on the life-history strategy of these birds also in the Carpathian Basin. In the future, based on the above results, I plan to continue to study the dispersal, timing of breeding and age at first reproduction in collared flycatchers and also reveal their patterns in the aspect of climatic conditions.

Published papers

Jablonszky M., Szász E., Krenhardt K., Markó G., Hegyi G., Herényi M., Laczi M., Nagy G., Rosivall B., Szöllősi E., Török J., Garamszegi L.Zs. 2018 Unravelling the relationships between life history, behaviour and condition under the pace-of-life syndromes hypothesis using long-term data from a wild bird. *Behavioral Ecology and Sociobiology* 72: 52.

Laczi M., Garamszegi L.Zs., Hegyi G., Herényi M., Ilyés G., Könczey R., Nagy G., Pongrácz R., Rosivall B., Szöllősi E., Tóth L., Török J. 2019 Teleconnections and local weather orchestrate the reproduction of tit species in the Carpathian Basin. *Journal of Avian Biology* in press

Szász E., Jablonszky M., Krenhardt K., Markó G., Hegyi G., Herényi M., Laczi M., Nagy G., Rosivall B., Szöllősi E., Török J., Garamszegi L.Zs. 2019 Male territorial aggression and fitness in collared flycatchers: a long-term study. *The Science of Nature* 106: 11.

Manuscripts in submission

Herényi M., Garamszegi L.Zs., Hargitai R., Hegyi G., Laczi M., Markó G., Nagy G., Rosivall B., Szöllősi E., Török J. - The role of reproductive performance, food availability and male characteristics in the survival of collared flycatchers. (in submission to *Behavioral Ecology and Sociobiology*)

Jablonszky M., Krenhardt K., Markó G., Szász E., Hegyi G., Herényi M., Kötél D., Laczi M., Nagy G., Rosivall B., Török J., Garamszegi L.Zs. - A behavioural trait displayed in an artificial novel environment correlates with dispersal in a wild bird. (in submission to *Ethology*)

Conferences

Jablonszky M., Krenhardt K., Markó G., Szász E., Hegyi G., Herényi M., Laczi M., Nagy G., Rosivall B., Török J., Garamszegi L. Zs. 2018: Az örvös légykapó (*Ficedula albicollis*) mesterséges környezetben mutatott viselkedésének biológiai relevanciája: konzisztens egyedi különbségek és diszperziós mintázatok. Magyar Etológiai Társaság XX. Konferenciája, Kolozsvár, Románia

Herényi M., Garamszegi L.Zs., Hargitai R., Hegyi G., Laczi M., Nagy G., Rosivall B., Szöllősi E., Török J. 2017: Survival costs of reproduction and the role of food availability in the collared flycatcher. 11th Conference of the European Ornithologists' Union, Turku, Finland