Final Project Report

FK124414 „Mother knows best: Maternal programming of migratory behaviour”

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The main goal of this early career research grant was to better understand the regulation of migratory behaviour, particularly the role environmental stress plays via the parents on the migratory phenotype of the offspring. I used a partial migrant (i.e., when both migrant and resident individuals occur in the same breeding population) species, the Eurasian blackbird (Turdus merula) as a model species.

First, I analyzed a long-term ring recovery data set (obtained from the Hungarian Ringing Center) and confirmed that indeed, the Eurasian blackbird is a partial migrant in Hungary, and equally importantly, the average migration distance of the population is continuously declining, which, given the effects of urbanization and climate warming, may lead to a completely resident population in the near future (Németh 2007). These results make it even more important to better understand the ecological and evolutionary processes that maintain migratory behaviour in a population.

Field monitoring of migratory strategies, physiology, reproductive success and survival: During the project period (2017-2023), we colour-ringed 1209 blackbirds (including adults, juveniles and nestlings) and looked for marked individuals each week to ultimately determine the migration strategy of the individuals. We recaptured 202 individuals and made over 3000 resightings of colour-ringed individuals in different times of the year. The study areas included sites along an urbanization gradient in Debrecen, Hungary, from inner city residential apartment complexes through university campuses, parks and a botanical garden reaching into the surrounding Great Forest Nature Reserve. (Because of our urban-forest gradient arrangement of study sites, students were able to compare parameters of reproductive success and nesting biology across areas with different degrees of urbanization and earned them best poster prize and honorable mention in a poster contest at an urbanization-themed scientific conference in 2018.) We had resighted 57% of the birds that were born or bred here at least once. Most of them were residing in urban areas, living a resident lifestyle, a smaller proportion used the urban areas in the winter but bred in the Great Forest Reserve (still employing a resident strategy), and the smallest proportion of the birds appeared to be migratory, breeding at one of the study sites and supposedly migrating for the winter (as they were not detected during our weekly resighting surveys). As a result of ring recoveries (recaptures, dead recoveries and resightings of colour-ringed individuals), we were able to use capture-recapture models to estimate survival probabilities in different sex and age groups employing different migratory strategies (assigned based on ring recoveries). We were also able to link premigratory corticosterone titers to migratory life-history, as well as estimate the effect of migratory strategy on (in a limited number of cases lifetime) reproductive success. This work is part of the PhD dissertation research

program of two students, Noémi Pallás and Ivan Gonzalez, and there are two manuscripts being prepared in relation to this 6-year dataset, one addressing the links between migratory strategy, endocrine profile and survival, while the other investigates the effects of urbanization on migratory life history and reproductive success.

Maternal stress manipulation experiment: Our early problems (see below) with capturing nest building females to manipulate maternal stress levels prior to egg laying had been eventually resolved by exposing them to (nest)predator vocalization playbacks, which is supposed to increase corticosterone levels and affect the phenotype of the developing offspring. This experiment therefore started later, in 2019, and after a year of hiatus due to the pandemic in 2020, it continued in 2021 and 2022. Due to the high nest mortality/predation rates across different habitats (65-80%), multiple years of experimental manipulations were needed to reach acceptable sample size for tracked offspring. However, our results showed no effect on maternal investment or offspring movement patterns and propensity to migrate as a response to predator vocal cue treatment of the mothers. Manuscript from this work is being prepared for submission at the moment.

Difficulties: In the first year of the project, we realized that manipulating female hormone levels prior to egg laying in a free living blackbird is very difficult due to our inability to catch most females on time and without inadvertently causing nest abandonment. We modified the experimental protocol to include predator vocal calls in the environment during egg-laying to induce elevated maternal stress levels. The covid pandemic caused another difficult period when due to the lockdown regulations, students could not attend the university or go out to do field work. Finally, the Russian-Ukraine war prevented us to continue to use the ICARUS satellite tags to track blackbirds as signals stopped coming from the Russian operated International Space Station. All this prompted me to ask for a no cost two-year extension, which was granted so we could finish our field experimental work and tracking project to assess the effects of the experimental treatments. Due to this delay with collecting the field data, with which we were supposed to parameterize the models of maternal effects on migratory strategies, the modeling work is being delayed and have only just started. That is why I am not able to provide results on the third component of the proposal.

The following popular science article was also published during the project period:

Németh Zoltán: Emberpajzs-hatás: a ragadozó-zsákmány-kapcsolatok átalakulása túlnépesedő világunkban. *Varázslatos Magyarország*, 2023/2. 61-63. old.

This research grant also gave me the opportunity to complete and contribute to the publication of earlier and continuing projects, some of which are closely related to the general topic of this grant, stress physiology and the regulation of migratory behavior, for which I include summaries below.

Partial migration and decreasing migration distance in the Hungarian population of the Common Blackbird (Turdus merula Linnaeus, 1758): Analysis of 85 years of ring recovery data

Zoltán Németh

Ornis Hungarica, 25 (1):101-108. (2017)

The Common Blackbird is a partial migrant throughout much of its range in Europe. That is, part of its breeding population migrates while the rest stays at the breeding ground for winter. Given the rapidly changing global climate, it is important to understand how migratory birds, including partial migrants, respond to shifting climatic conditions. In this study, I analyzed 85 years of ring recovery data of the Hungarian population of the Blackbird, ringed during the breeding season and recovered during migration or winter, with two objectives in mind: (1) to assess whether the Hungarian Blackbird population is also partially migratory, and (2) to test the prediction that Blackbirds have exhibited decreasing migration distances over the past decades as expected based on warming winter temperatures. Hungarian Blackbirds expressed both migratory and resident strategies, thus can be considered as partial migrants. Furthermore, Blackbirds had been recovered increasingly closer (-5.9 km/year) to their breeding grounds in the past decades. Age and sex had no effects on recovery distance. Provided that this trend continues, the adaptive benefits of migratory behavior may eventually be reduced to a level that selection will not maintain it in the population and the Hungarian population becomes entirely sedentary. Surprisingly, 88% of migrant recoveries were the result of shooting or hunting activities in Mediterranean countries, primarily in Italy, highlighting both the need to understand the effects of hunting pressure on migratory behavior at the population level in songbirds and the urgency to ban the killing of migratory birds in European countries.

Behavioral and physiological traits of migrant and resident white-crowned sparrows: a common garden approach

Marilyn Ramenofsky, Andrew W Campion, Jonathan H Pérez, Jesse S Krause, Zoltán Németh

Journal of Experimental Biology, 220 (7): 1330-1340. (2017)

To accommodate a migratory life history, migrants express a greater number of physiological and behavioral stages per annum than residents and are thus considered to have higher finite state diversity (FSD). To investigate the physiological mechanisms and constraints associated with migration, direct comparison of two subspecies of white-crowned sparrow – migrant, Zonotrichia leucophrys gambelii, and resident, Z. l. nuttalli – were made under common garden conditions of photoperiod and housing, as birds progressed from winter through the vernal life history stages. We tested the hypothesis that migrants (higher FSD) respond differently than residents (lower FSD) to the initial predictive cue, photoperiod, to initiate and integrate the progression of vernal stages of prenuptial molt, migration and development of breeding. If differences in vernal phenology were noted, then the basis for the distinctions was considered genetic. Results indicate that (1) residents had a lower threshold to vernal photoperiod with elevations of plasma androgen, growth and development of reproductive structures preceding those of migrants; (2) only migrants displayed prenuptial molt, preparations for migration and migratory restlessness; and (3) neither baseline nor stress-induced plasma corticosterone differed across subspecies, suggesting energetic demands of the common garden were insufficient to induce a differential adrenocortical response in either subspecies, highlighting the impact of environmental conditions on corticosterone secretion. Thus, in a common garden experiment, Z. l. gambelii responds differently to the initial predictive cue, photoperiod, to initiate and execute the vernal stages of molt, migration and development of breeding in comparison to the shared stage of breeding with Z. l. nuttalli, confirming a genetic basis for the subspecies differences.

Inter-laboratory variation in corticosterone measurement: Implications for comparative ecological and evolutionary studies

Kerry V. Fanson, Zoltán Németh, Marilyn Ramenofsky, John C. Wingfield, Katherine L. Buchanan

Methods in Ecology and Evolution, 8:1745–1754. (2017)

1. Interspecific comparisons of endocrine data are useful for drawing broad conclusions concerning the role of ecological variables in the evolution of physiological pathways. However, comparisons of endocrine data generated by different research groups are problematic, due to inter-laboratory variation in measured hormone values. To date, we know of no study which has quantified the extent of inter-laboratory variation in the measurement of hormone levels, outside of biomedical studies.
2. To evaluate the extent to which laboratories differ in their measurement of hormones, we prepared seven samples of avian plasma with known concentrations of corticosterone and sent them for blind analyses to 19 laboratories and asked them to report the methods used and the values obtained.
3. Both absolute hormone concentrations and the ratios between samples were equally variable, up to an order of magnitude different for some concentrations. Laboratory identity accounted for more than 80% of the variation in reported corticosterone, but we could not identify any methodological factors that consistently contributed to this inter-laboratory variation. In addition, laboratory measurement error was significantly correlated with the latitude of the primary study species for each laboratory, suggesting that inter-laboratory variation has the potential to drive trends in corticosterone datasets.
4. Inter-laboratory variation in corticosterone measurement may have serious implications for quantitative comparisons of endocrine values across laboratories, although comparisons of qualitative patterns may be more robust because rank order of the samples was relatively consistent across laboratories. Ignoring laboratory effect and the non-independence of data may lead to an inflated rate of Type I error and spurious correlations.

Migration pattern of Gambel's White-crowned Sparrow along the Pacific Flyway

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Journal of Ornithology, 160: 1097–1107. (2019)

White-crowned Sparrow (Zonotrichia leucophrys) populations of western North America exhibit dramatic differences in life history strategies including migration behavior. However, individual migration strategies and population-level migratory patterns remain largely unknown for this species. Here, we focused on the long-distance migratory subspecies, Gambel's White-crowned Sparrow (Zonotrichia leucophrys gambelii). We used ringing, tracking and stable hydrogen isotope (δ2H) analysis of individuals migrating along the Pacific Flyway to assess individual phenology and routes as well as the pattern of connectivity between breeding and non-breeding sites. Results from all three methods, consisting of 79 ring recoveries, four light level geolocator tracks and 388 feather δ2H values, indicate low degrees of migratory connectivity. The isotope data provide evidence for leapfrog migration with the more southerly populations traveling greater distances to the breeding grounds than more centrally wintering individuals. Location estimates of four annual journeys revealed individually consistent migration strategies with relatively short flight bouts separated by two to three and two to six stopover sites during spring and autumn migration, respectively. However, combined results from all methods indicate high variability in migration distance among individuals. These findings confirm the phenotypic flexibility observed within this species and highlight the potential of White-crowned Sparrows for further investigations of evolutionary adaptations to ongoing changes in the environment.

Annual regulation of adrenocortical function in migrant and resident subspecies of white-crowned sparrow

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Hormones and Behavior, 127: 104884, (2021)

Corticosterone affects physiology and behavior both during normal daily processes but also in response to environmental challenges and is known to mediate life history trade-offs. Many studies have investigated patterns of corticosterone production at targeted times of year, while ignoring underlying annual profiles. We aimed to understand the annual regulation of hypothalamic-pituitary-adrenal (HPA) axis function of both migrant (*Zonotrichia leucophrys gambelii*; n = 926) and resident (*Z.* l. *nutalli*; n = 688) subspecies of white-crowned sparrow and how it is influenced by environmental conditions – wind, precipitation, and temperature. We predicted that more dramatic seasonal changes in baseline and stress-induced corticosterone would occur in migrants to precisely time the onset of breeding and cope with environmental extremes on their arctic breeding grounds, while changes in residents would be muted as they experience a more forgiving breeding schedule and comparatively benign environmental conditions in coastal California. During the course of a year, the harshest conditions were experienced the summer breeding grounds for migrants, at which point they had higher corticosterone levels compared to residents. For residents, the winter months coincided with harshest conditions at which point they had higher corticosterone levels than migrants. For both subspecies, corticosterone tended to rise as environmental conditions became colder and windier. We found that the annual maxima in stress-induced corticosterone occurred prior to egg lay for all birds except resident females. Migrants had much higher baseline and acute stress-induced corticosterone during breeding compared to residents; where in a harsher environment the timing of the onset of reproduction is more critical because the breeding season is shorter. Interestingly, molt was the only stage within the annual cycle in which subspecies differences were absent suggesting that a requisite reduction in corticosterone may have to be met for feather growth. These data suggest that modulation of the HPA axis is largely driven by environmental factors, social cues, and their potential interactions with a genetic program.

Biological Earth observation with animal sensors

Jetz, Walter; Tertitski, Grigori; Kays, Roland; Mueller, Uschi; Wikelski, Martin; Åkesson, Susanne; Anisimov, Yury; Antonov, Aleksey; Arnold, Walter; Bairlein, Franz et al.

Trends in Ecology and Evolution 37 (4): 293-298., 6 p. (2022)

Space-based tracking technology using low-cost miniature tags is now delivering data on fine-scale animal movement at near-global scale. Linked with remotely sensed environmental data, this offers a biological lens on habitat integrity and connectivity for conservation and human health; a global network of animal sentinels of environmental change.

Local weather and endogenous factors affect the initiation of migration in short- and medium-distance songbird migrants

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Journal of Avian Biology 2023 (3-4): e03029, 19 p. (2023)

Migratory birds employ a variety of mechanisms to ensure appropriate timing of migration based on integration of endogenous and exogenous information. The cues to fatten and depart from the non-breeding area are often linked to exogenous cues such as temperature or precipitation and the endogenous program. Shorter distance migrants should rely heavily on environmental information when initiating migration given relatively close proximity to the breeding area. However, the ability to fatten and subsequently depart may be linked to individual circumstances, including current fuel load and body size. For early and late departing migrants, we investigate effects of temperature, precipitation, lean body mass, fuel load and day of year on the initiation of migration (i.e. fuel load and departure timing) from the non-breeding region by analyzing 21 years of banding data for four species of short- and medium-distance migrants. Temperatures at the non-breeding area were related to temperatures at potential stopover areas. Despite local cues being predictive of conditions further north, the amount variation explained by local weather conditions in our models differed by species and temporal period but was low overall (< 33% variation explained). For each species, we also compared lean body mass and fuel load between early and late departing migrants, which showed mixed results. Our combined results suggest that most individuals migrating short or medium distances in our study did not time the initiation of migration with local predictive cues alone, but rather other factors such as lean body mass, fuel load, day of year, which may be a proxy for the endogenous program, and those beyond the scope of our study also influenced the initiation of migration. Our study contributes to understanding which factors influence departure decisions of short- and medium-distance migrants as they transition from the non-breeding to the migratory phase of the annual cycle.

Multilevel climatic responses in migratory insects

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Ecological Entomology doi: 10.1111/een.13270 (2023)

Evidence is mounting that migration in ectotherms is more widespread than formerly believed. Thus, a number of insects living in temperate climates, including locusts, butterflies, moths and dragonflies, following seasonal migration strategies show high responsiveness to alterations in climatic processes, similar to a broad taxonomic range of birds. On global scales, migratory insects include iconic large butterflies, dragonflies and also a number of crop pests. However, insect migrations are ecologically distinct from those of vertebrates, often relying heavily on seasonal winds and multiple generations to complete a full annual cycle, due to short insect life spans.

Here, we review publicly available online resources to identify key patterns of spatial, taxonomic scales and complexity of climatic responsiveness to environmental predictors in migratory insects.

We found that migratory insects respond to various levels of complexity in climatic patterns, and these responses are predicted by life history and ecological traits: (i) responses to climatic effect type were predicted by climate zone(s) of the distribution area, whereas (ii) response to climatic complexity was predicted by body size. In conclusion, migratory insects respond to various levels of complexity in climatic processes, and this responsiveness is governed by a substantially wider array of environmental predictors than demonstrated in vertebrates.

Comparison of the phenotypic flexibility of muscle and body condition of migrant and resident White-crowned Sparrows

Ramenofsky, M.; A.W. Campion; D.T. Hwee; S. Wood; J.S. Krause; Z. Németh; J. H. Perez; S. Bodine

Ecological and Evolutionary Physiology (formerly Physiological and Biochemical Zoology) (accepted, manuscript ID: EEP-23010R3) (2024)

Seasonally breeding birds express variations of traits (phenotypic flexibility) throughout their life history stages that represent adaptations to environmental conditions. Changes of body condition during migration have been well studied, whereas, alterations of skeletal and cardiac muscles, body mass, and fat scores have yet to be characterized throughout the spring or fall migratory stages. Additionally, we identified flexible patterns of muscle, body mass, and fat score in migrant White-crowned Sparrows (Zonotrichia leucophrys gambelii) in comparison with resident subspecies (Z.l. nuttalli) during their shared stages to evaluate the influence of different life histories. Migrants showed hypertrophy of pectoralis muscle fiber area on the wintering grounds in late prealternate molt; yet, increased pectoralis muscle mass was not detected until birds readied for spring departure. While pectoralis profile and fat scores enlarged at predeparture in spring and fall, pectoralis, cardiac, and body masses were greater only in spring stages suggesting seasonal differences for migratory preparation. Gastrocnemius mass changed little across the stages; however, fiber area declined from winter though fall predeparture rebounding on the wintering grounds where migrants become more sedentary. In general, residents are heavier birds with larger leg structures while migrants sport longer wings and greater heart mass. Phenotypic flexibility was most prominent among residents with peaks of pectoralis, gastrocnemius, and body masses during the winter stage when local weather is most severe. Thus, the subspecies express specific patterns of phenotypic flexibility with peaks coinciding with stages of heightened energy demands: winter stage for residents and spring stages for migrants.