Final project report

For the grant # OTKA K113108

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Summary

In this project, we set out to investigate the physiological mechanisms related to the evolution of lifespan. We were particularly interested in the neuroendocrine mechanisms that affect resource allocation and thus the trade-off between reproduction and survival. We investigated how the pleiotropic peptide hormone, insulin-like growth 1 (IGF-1) and the glucocorticoid hormone, corticosterone affect growth, reproductive decisions and mortality in natural bird populations. We found that the hormonal response to stress (a trait that is thought to reflect allocation between self-maintenance and reproduction) varies with age and according to the energetic status of the individuals. We also found that IGF-1 also reacts to stress, and this response is independent from the glucocorticoid stress response. We showed that short-term increases in IGF-1 levels may induce oxidative stress, but are unlikely to affect survival on the long run. We demonstrated that IGF-1 levels regulate growth and may affect ageing. However, these responses may depend on the year and the study species. Altogether, this research project resulted in the development of a new immunoassay, and in the publication of 22 research papers and 4 additional conference abstracts. We also prepared 12 manuscripts that have been either submitted or will be submitted in the following months. Other data collected during the project is still being analyzed and therefore are expected to lead to new publications. We only summarize some key results below.

Assay development

One of the major challenges in this project was to develop a new analytical method for measuring IGF-1 from avian samples. In order to do that, first we tried to use commercially available assay kits. While we were able to use some of these kits to measure plasma IGF-1, other ones failed to detect any IGF-1 in the samples and in positive controls. Furthermore, undocumented changes in the assay kit components caused substantial lot-to-lot variation in the apparent sensitivity of the assay, thus questioning the reliability of the product. Questionable consistency combined with the high price of these commercial kits made us consider new alternatives of developing a reliable measurement technique for avian IGF-1.

First, we tried to set up an analytical method based on liquid chromatography tandem mass spectrometry (LC-MS). Several rounds of experimental trials and consultation with the leading experts of the technology failed to produce promising results, therefore we abandoned this approach and turned to our next target. Our next aim was to set up an immunoassay using commercially available antibodies. Since the amino acid sequence of avian IGF-1 is different from that of mammals, we initially tried to use commercial antibodies raised against avian IGF-1. We could find only one such product on the market, but it failed to bind IGF-1 from our plasma samples. We also tried several different heterologous antibodies, but most of them also did not produce the results we expected. Therefore, we started establishing a new immunoassay from scratch by starting producing our own antibody. We determined the nucleotide and amino-acid sequence of IGF-1 gene and

peptide, and synthesized the immunogen and started the immunization procedure. Unfortunately, even though our team included highly skilled experts in biochemistry and immunoassay development, we encountered many unexpected obstacles along the way that made the entire procedure much longer than what we had anticipated. Not detailing every technical issues and difficulties, after three rounds of immunization, we finally managed to produce a source of antibody that could be used as a basis for the development of an avian-specific and sensitive immunoassay. The next step was the assay validation procedure for our study species, which provided satisfactory results. We have now a working assay in both the enzyme-linked immunosorbent assay (ELISA) and the radioimmunoassay (RIA) format. The ELISA technique was used and described in our recent publication (Mahr et al. 2020), while a more detailed description of the RIA is under preparation (Lendvai et al. MS a).

We consider the **successful development of the avian IGF-1 assay as a major outcome of our project**. However, due to the numerous the difficulties that were beyond our control, this achievement was only realized by the end of the project. So while we performed experiments and collected data as originally planned, the measurement of these samples and the preparation of the manuscripts took place later than expected, therefore many of our results are still unpublished, in preparation or published not in their intended definitive form (e.g. a research paper), but were communicated e.g. at international conferences. However, due to the exclusivity of our avian IGF-1 assay, we have recently established a number of collaborations with other researchers and initiated a number of new projects that already produced interesting results (see below). Therefore, the current project is expected to spawn new results and publications even after the official closure of its term.

Physiological regulation of stress response, mortality, oxidative stress and reproductive decisions

Lifespan is determined by physiological mechanisms that affect the allocation to self-maintenance and thus survival. One of the proximal mechanisms affecting survival is oxidative stress. Neuroendocrine pathways that regulate resource allocation in face of changes in environmental conditions have been recognized to play a crucial role in oxidative balance and survival. Among these mechanisms, the best studied are glucocorticoid hormones. Here, in a series of experiments, we investigated the complex role that glucocorticoids play in regulating self-maintenance.

Hormonal regulation of allocation trade-offs throughout lifespan

First, using data collected earlier on two species with contrasting life history, **we investigated how age, a major state variable affected individuals' hormonal response to a standardized stressor: a trait that may reflect allocation between self-maintenance and reproduction**. We measured hormonal (corticosterone) response to capture stress in consecutive years. In the short-lived house sparrows, we found that birds responded less strongly to capture stress as they grew older. These results suggest that stress responsiveness is a plastic trait that may vary within individuals in an adaptive manner, and natural selection may act on the reaction norms producing optimal phenotypic response in the actual environment and life-history stage. We published these results in (Lendvai et al. 2015). In the very long-lived snow petrels, we tested the same question, by extending the analyses with information about the current energetic status of the individuals. Incubating snow petrels parents alternate incubation duties, and while one parent is foraging in the sea its partner remains on the nest incubating the eggs while fasting. This biological system gave us the opportunity to test

how energetic constraints affect the relationship between the age and the physiological response to stress. We found that the corticosterone stress response was decreased in old petrels, but only when they were in good condition (not fasting). This pattern was different in fasting petrels, where corticosterone response did not decrease with age of the birds. At the ultimate level, old individuals may maintain a strong corticosterone stress response when fasting because the survival costs of increased stress resistance and parental effort might then outweigh their reproductive benefits. We published these results in (Angelier et al. 2020).

Phenotypic integration of physiological mechanisms

Second, **we investigated the phenotypic integration of different hormonal axes and fitness-related physiological metrics**. We investigated how natural variation in glucocorticoid hormone levels, oxidative stress measurements, and condition related to each other in two breeding songbirds. In the tree swallow we tested whether any of these traits predicted the probability of a particular individual's return to the local population in the following two years, an indicator of survival in this philopatric species. We found that males and females with longer telomeres had lighter nestlings. Moreover, individuals with lower plasma antioxidant capacity and higher reactive oxygen metabolites (i.e., greater oxidative stress) were less likely to return to the population. However, none of these traits were related to glucocorticoid levels. **Our findings suggest a trade-off between reproduction and survival, with individuals with shorter telomeres having heavier nestlings but potentially paying a cost in terms of higher oxidative stress and lower survival**. These results were published in (Ouyang et al. 2016).

In another breeding songbird, the house sparrow, we studied the relationship between body condition, two neuroendocrine hormones (corticosterone and insulin-like growth factor 1, IGF-1) as physiological regulators, and two physiological systems related to resource metabolism (glucose) and oxidative balance (malondialdehyde, MDA). We measured these variables under baseline and stress-induced conditions. We used path analysis to analyze different scenarios about the structure of the physiological network. We found that individuals in better condition had lower corticosterone levels, corticosterone and IGF-1 levels are positively associated, and oxidative damage is higher when levels of corticosterone, IGF-1 and glucose are elevated. After exposure to stress, these relationships were considerably reorganized. In response to stress, birds increased their corticosterone and glucose levels, and decreased their IGF-1 levels. However, individuals in better condition increased more their corticosterone levels and maintained more their IGF-1 levels in response to stress. The stress-induced changes in corticosterone and IGF-1 levels were associated with an increase in glucose levels, which in turn was associated with a decrease in oxidative damage. **This is the first time that the relationship between IGF-1, oxidative stress and glucose has been tested in free-living organisms.** The manuscript reporting these results has been submitted for publication (Vágási et al. MS a).

In a third songbird species, the bearded reedling, we experimentally tested the relationships between the glucocorticoid stress response axis and the IGF-1 mediated hormonal axis. In this study, we combined field observations with a controlled experiment to investigate how circulating levels of IGF-1 change in response to stress and whether this change is due to concomitant change in glucocorticoids. We showed that corticosterone levels significantly increased while IGF-1 levels significantly decreased during capture and handling stress. However, change in corticosterone levels were not related to change in IGF-1 levels. In the controlled experiment, we used a non-invasive oral manipulation of corticosterone on undisturbed birds to separate the effects of stress from corticosterone. Experimentally elevated corticosterone levels did not affect IGF-1 levels. **These**

results are the first to highlight that circulating IGF-1 levels are responsive to stress independently from glucocorticoids and suggest that the HPS axis is an autonomous physiological pathway that may play an important role as regulator of life-history decisions. We published these results in (Tóth et al. 2018).

The role of IGF-1 in regulating growth, ageing and survival

We tested the causal role that IGF-1 may play in the regulation of lifespan, possibly through its effects on oxidative stress as it was suggested in the literature. However, these effects have no experimental evidence in wild animals. We implanted bearded reedlings, with microspheres filled with exogenous IGF-1, which elevated the circulating IGF-1 levels for at least 24h. **We showed for the first time that in response to experimental elevation of circulating IGF-1 levels, individuals originating from a wild population experienced increased levels of oxidative damage at short-term** (Fig. 1). This result is consistent with a previous correlational study where circulating baseline levels of IGF-1 were found to be positively associated with MDA in adult house sparrows (Vágási et al. MS a). The treatment had no effect on survival over 16 months; however, birds with higher pre-treatment (baseline) IGF-1 levels had better survival prospects. **These results suggest that, although high IGF-1 levels may induce oxidative damage, natural variation in this hormone level may reflect the outcome of individual optimization.** These results were submitted for publication (Lendvai et al. MS b).

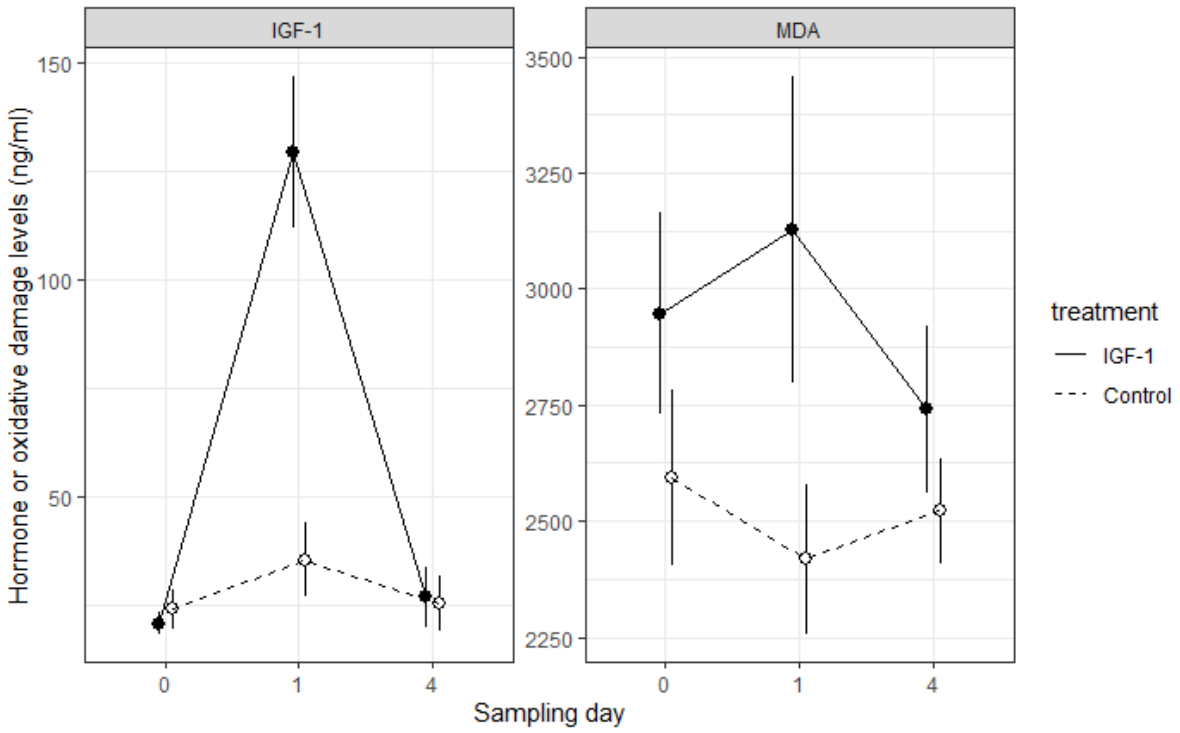

Figure 1. Subcutaneous injection with IGF-1-loaded microspheres resulted in a significant increase in circulating IGF-1 and oxidative damage (MDA) levels measured 24 h later (day 1) in captive bearded reedlings, but these effects disappeared by day 4. Mean ± SE.

In bearded reedlings, we also collected several hundred samples from adults and juveniles to analyze seasonal variation of IGF-1 levels, relationship with growth and survival. Due to the large number of

the samples, hormone measurements and analyses are still being performed. However, the relationship between IGF-1 and growth were also investigated in two experimental studies.

First, in collaboration with researchers from the North Dakota State University we set out to test whether IGF-1 accelerates growth and cellular aging. We manipulated circulating IGF-1 in house sparrow nestlings during the post-natal growth period over a period of three years (2016-2018). Nestlings within nests were assigned to either an experimental or control treatment. Experimental nests were injected with a physiologically relevant dose of recombinant human IGF-1 (rhIGF-1) in a gelatin carrier matrix from day 3- day 10 post-hatch. Control nestlings were injected with only the gelatin carrier matrix. To measure IGF-1 levels and telomere length, blood samples were collected at day 3, 6, and 10 post-hatching. We collected growth measurements every 3 days until day 10 post-hatch in all years. Nestling IGF-1 levels were successfully raised following an injection of rhIGF-1. Experimental chicks had longer culmens than controls in all years. However, feather development and growth rate were only significantly greater than controls in 2016. Nestling growth rates did not differ between treatments in 2017 or 2018. However, in 2016 and 2018, experimental birds were significantly heavier than controls at their final mass. Further, in 2016, IGF-1 injected nestlings had significantly shorter telomeres at day 10 post-hatching than controls, but there was no significant relationship between treatment and nestling telomere length in 2017 and 2018 at day 10 post-hatch. However, at day 12 post-hatch experimental birds had significantly shorter telomeres than controls in 2018. **Overall, the results of this study suggest that IGF-1 may impact nestling growth and telomere dynamics**, however, the degree to which IGF-1 affects these traits varies according to changes in environmental conditions (years). These results were first published in a doctoral thesis (Sirman, 2019), and are now being prepared for submission into research journals. We plan to publish two separate papers, one detailing natural variation of IGF-1 in relationship with growth (Sirman et al. MS a) and sex and another paper on the experimental results (Sirman et al. MS b).

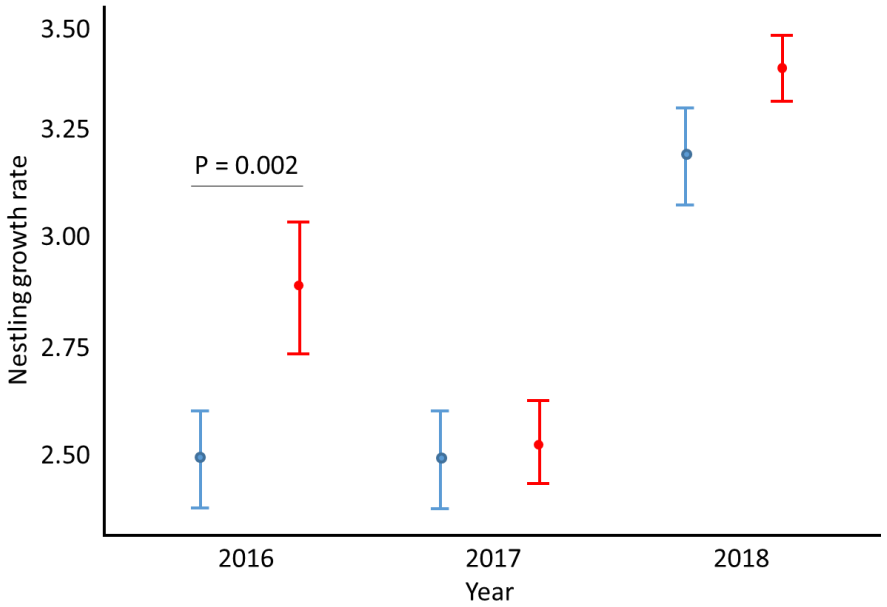

Figure 2. The relationship between growth rate (mean ± SE) and treatment (blue: control, red: IGF-1 treatment) by year in house sparrow nestlings during post-natal development. Growth rate was calculated as the slope of the change in mass with age from day 2 to day 8 post-hatch for each nestling. P-values are based on Tukey's HSD post-hoc test and significant differences

Second, in collaboration with researchers at the University of Glasgow, we conducted an experimental manipulation in zebra finch nestlings modifying their early-life growth dynamics, i.e. reducing or accelerating their growth. In addition, we obtained longitudinal blood samples at different time points from hatching to adulthood for measuring the plasma IGF-1 levels and the red blood cells' telomere length, an established lifespan marker in this species. While treatment affected growth curves, this variation was not related to IGF-1 levels and to telomere lengths. These results were first presented at the 19th European Ornithologist Union (Salmon et al. 2019) and now we are preparing the manuscript for submission (Salmon et al. MS).

Finally, in collaboration with researchers from the University of Aberdeen, we studied alpine swifts. We found that in 50 days old nestlings, IGF-1 is decreasing with wing length. Nestlings with a short wings at 50 days are likely to still show feather growths whereas nestlings with long wings have finished growing their feathers. In adults, we found that larger individuals (longer wings and sternum length) had higher IGF-1 levels. Interestingly, higher IGF-1 levels were also associated with shorter telomere lengths, after controlling for age (Figure 3.). We are preparing the results for publication (Bize et al. MS).

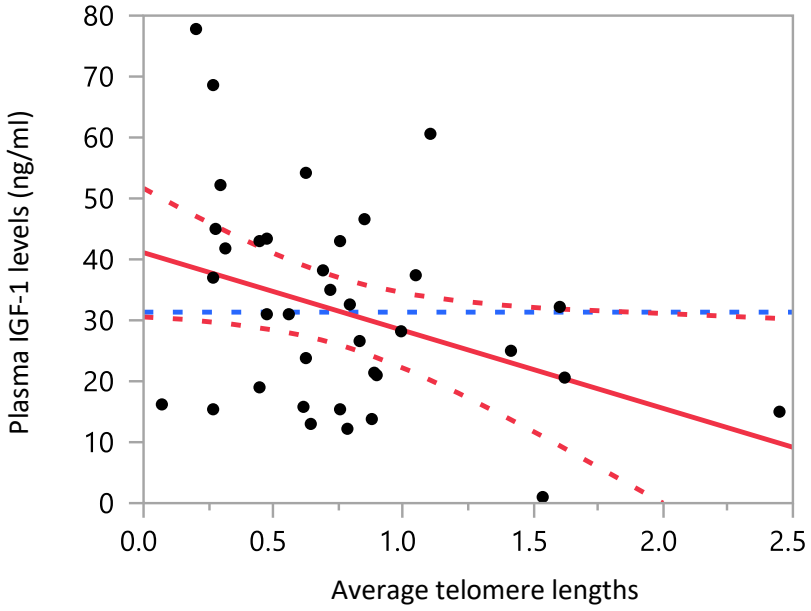

Figure 3. Higher plasma IGF-1 levels are associated with shorter telomere lengths in adult alpine swifts.

The role of IGF-1 in ornament expression

To investigate how IGF-1 affects ornament expression, we performed an observational field study and an experimental study. In the field study, we investigated whether IGF-1 levels during molting predict the elaboration of multiple ornamental plumage traits in male and female bearded reedlings. We collected blood samples of males and females shortly before the molting completed and measured the size and colors of ornamental traits. We show that in males, structural plumage colors, the size of the melanin based ornament (beard) and tail length are independent traits. IGF-1 levels are associated with the length of the tail and the expression of male structural plumage components (UV-coloration), but not the melanin based ornament. **Our results indicate that higher IGF-1 levels had positive effects on male structural plumage colors and tail feather length (Figure 4). This is the**

first study, showing a potential role of IGF-1 in the expression of plumage ornaments in a bird species. Our findings suggest that IGF-1 might serve as an ideal candidate to study the mechanisms linking condition and the capacity to develop sexually selected ornaments. These results were accepted for publication (Mahr et al. 2020).

In the experimental study, we manipulated circulating IGF-1 levels in captive juvenile bearded reedlings while they were naturally molting into their first adult plumage. IGF-1 manipulation did not affect the growth of primary feathers, and did not affect the final ornaments. These negative results may be due to the short duration of the manipulation, which may not have been sufficient to affect the development of the new ornaments. These results will be submitted shortly for publication (Lendvai et al. MS c).

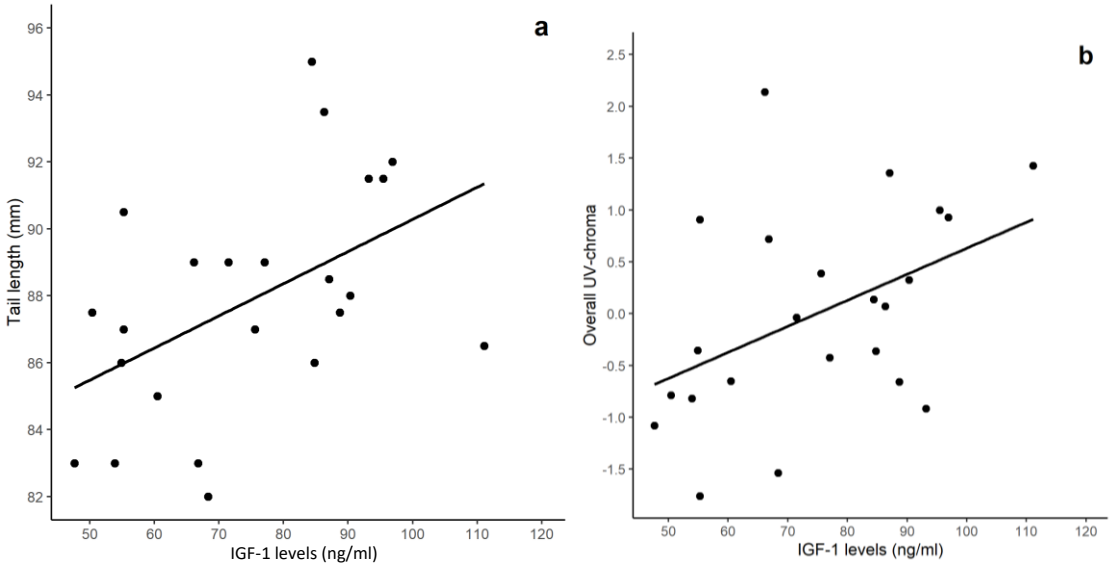

Figure 4. Baseline IGF-1 levels during molt are related to sexually selected ornaments in male bearded reedlings. Males with higher IGF-1 levels have (a) longer tails and (b) develop plumage with higher reflectance in the UV-range.

Physiological correlates of interspecific variation in lifespan

Lifespan is expected to be affected by IGF-1, potentially through its effects on oxidative balance. In order to test the effects of IGF-1 and oxidative stress on interspecific variation in lifespan, we collected baseline plasma samples from more than 150 bird species over three years. Compared to other studies, this dataset only includes samples from breeding individuals. Also, every sample was collected shortly after capture, and handling time until blood sample collection is known in each case. Therefore, this dataset avoids the problems inherent in some comparative studies, where differences in life history stages or large variations of handling-related stress may confound the data. Due to the large number of samples and to the difficulties with the hormone assays, IGF-1 measurement of these samples is still under way. However, **we have published a paper that shows for the first time that bird species with longer lifespan have higher nonenzymatic antioxidant capacity and suffer less oxidative damage to their lipids**. These results reinforce the role of oxidative

stress in the evolution of lifespan and also corroborate the role of oxidative state in the evolution of life histories among free-living birds. (Vágási et al. 2019).

At the interspecific level, we also investigated another proximate mechanism potentially strongly affecting mortality (and thus lifespan), the immune system. We investigated whether the sex differences in mortality is mirrored by differences in immune parameters (white blood cell counts and immune response variables). We showed that while overall, there was no sex bias in immunity, immune system of the males become weaker than that of females during the breeding season. We have prepared a manuscript reporting these results, which is now ready for submission (Valdebenito et al. MS).

Modelling the optimal response to changing environmental conditions

To understand the evolution of a regulatory mechanism that influences reproductive investment and somatic maintenance, we built an optimal routine model that investigates allocation decisions to reproduction, reserves and physiological repair under fluctuating food availability. The model allows incorporating the effect of adult mortality on optimal strategies while implicitly taking into account the metabolic costs associated with reproduction, maintaining reserves and physiological repair. The model predicts that the combination of two factors: adult background mortality and metabolic costs of maintenance affect optimal levels of maintenance, as well as the optimal upregulation of maintenance in response to one form of environmental stress (resource shortage) (Figure 5). While these results did not warrant a stand-alone publication, we used predictions of from this model to investigate variation in asexual reproduction, stress tolerance and the underlying genetic mechanisms (expression of key antioxidant genes, heat-shock proteins and elements of the insulin/IGF signalling pathway) in a cnidarian model system (*Hydra vulgaris*). The results of this study were published in (Sebestyén et al. 2017).

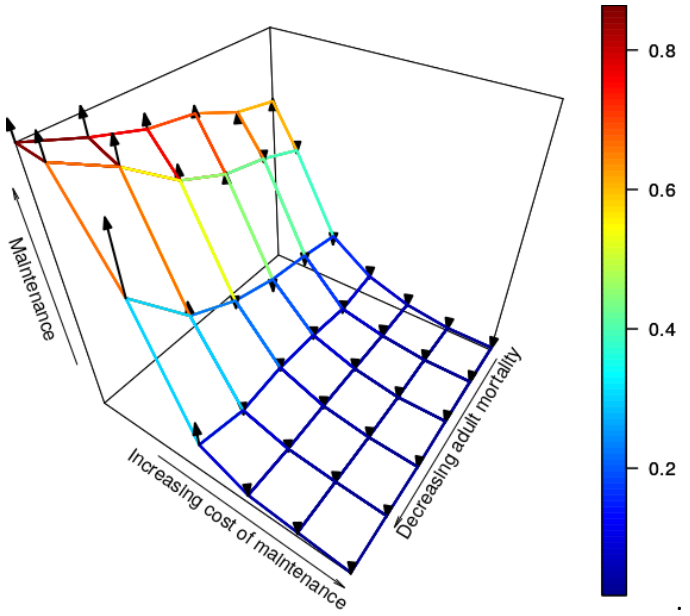

Figure 5. The effect of adult mortality rate and metabolic cost of maintenance on optimal maintenance levels in fluctuating environments with a high autocorrelation. The grid nodes show maintenance levels during periods with low food availability. Arrows point to maintenance levels during resource shortage. Maintenance is higher when adult mortality and the cost of maintenance are both low. Under these conditions, upregulation of maintenance during resource shortage is an optimal strategy

Research papers published during the project:

Akçay Ç, Lendvai ÁZ, Stanback MT, et al (2016) Strategic adjustment of parental care in tree swallows: life-history trade-offs and the role of glucocorticoids. Royal Society Open Science 3:160740. https://doi.org/10.1098/rsos.160740

Angelier F, Chastel O, Lendvai AZ, et al (2020) When do older birds better resist stress? A study of the corticosterone stress response in snow petrels. Biol Lett 16:20190733. https://doi.org/10.1098/rsbl.2019.0733

Cox AR, Robertson RJ, Lendvai ÁZ, et al (2019) Rainy springs linked to poor nestling growth in a declining avian aerial insectivore (Tachycineta bicolor). Proceedings of the Royal Society B: Biological Sciences 286:20190018. https://doi.org/10.1098/rspb.2019.0018

Dakin R, Ouyang JQ, Lendvai ÁZ, Haussmann MF, Moore IT, Bonier F (2016) Weather matters: begging calls are temperature- and size-dependent signals of offspring state. Behaviour 153:871–896. doi: 10.1163/1568539X-00003370

Lendvai ÁZ, Akçay Ç, Ouyang JQ, et al (2015a) Analysis of the optimal duration of behavioral observations based on an automated continuous monitoring system in tree swallows (Tachycineta bicolor): is one hour good enough? PLOS ONE 10:e0141194. https://doi.org/10.1371/journal.pone.0141194

Lendvai ÁZ, Akçay Ç, Stanback M, et al (2018) Male parental investment reflects the level of partner contributions and brood value in tree swallows. Behav Ecol Sociobiol 72:185. https://doi.org/10.1007/s00265-018-2594-3

Lendvai ÁZ, Giraudeau M, Bókony V, et al (2015b) Within-individual plasticity explains age-related decrease in stress response in a short-lived bird. Biology Letters 11:20150272. https://doi.org/10.1098/rsbl.2015.0272

Mahr K, Vincze O, Tóth Z, Hoi H, Lendvai ÁZ (2020) Insulin-like growth factor 1 is related to the expression of plumage traits in a paserine species. Behavioral Ecology and Sociobiology in press:

Montreuil-Spencer C, Schoenemann K, Lendvai ÁZ, Bonier F (2019) Winter corticosterone and body condition predict breeding investment in a nonmigratory bird. Behav Ecol arz129. https://doi.org/10.1093/beheco/arz129

Mougeot F, Lendvai ÁZ, Martínez-Padilla J, et al (2016) Parasites, mate attractiveness and female feather corticosterone levels in a socially monogamous bird. Behav Ecol Sociobiol 70:277–283. https://doi.org/10.1007/s00265-015-2048-0

Ouyang JQ, Lendvai ÁZ, Dakin R, et al (2015) Weathering the storm: parental effort and experimental manipulation of stress hormones predict brood survival. BMC Evolutionary Biology 15:219. https://doi.org/10.1186/s12862-015-0497-8

Ouyang JQ, Lendvai ÁZ, Moore IT, et al (2016) Do Hormones, Telomere Lengths, and Oxidative Stress form an Integrated Phenotype? A Case Study in Free-Living Tree Swallows. Integr Comp Biol 56:icw044. https://doi.org/10.1093/icb/icw044

Pap PL, Vincze O, Fülöp A, et al (2018) Oxidative physiology of reproduction in a passerine bird: a field experiment. Behav Ecol Sociobiol 72:18. https://doi.org/10.1007/s00265-017-2434-x

Pap PL, Vincze O, Wekerle B, et al (2017) A phylogenetic comparative analysis reveals correlations between body feather structure and habitat. Functional Ecology 31:1241–1251. https://doi.org/10.1111/1365-2435.12820

Sebestyén F, Póliska S, Rácz R, et al (2017) Insulin/IGF Signaling and Life History Traits in Response to Food Availability and Perceived Density in the Cnidarian Hydra vulgaris. Zoological Science 34:318–325. https://doi.org/10.2108/zs160171

Sepp T, Desaivre S, Lendvai AZ, et al (2018) Feather corticosterone levels are not correlated with health or plumage coloration in juvenile house finches. Biol J Linn Soc 124:157–164. https://doi.org/10.1093/biolinnean/bly029

Szép T, Dobránszky J, Møller AP, Dyke G, Lendvai ÁZ (2019) Older birds have better feathers: A longitudinal study on the long-distance migratory Sand Martin, Riparia riparia. PLOS ONE 14:e0209737. https://doi.org/10.1371/journal.pone.0209737

Szöllősi E, Tóth Z, Mahr K, Hoi H, Lendvai ÁZ (2019) Extremely low malaria prevalence in a wetland specialist passerine. Parasitology 1–9. https://doi.org/10.1017/S0031182019001215

Tartu S, Bustamante P, Angelier F, et al (2016) Mercury exposure, stress and prolactin secretion in an Arctic seabird: an experimental study. Funct Ecol 30:596–604. https://doi.org/10.1111/1365-2435.12534

Tóth Z, Ouyang JQ, Lendvai ÁZ (2018) Exploring the mechanistic link between corticosterone and insulin-like growth factor-1 in a wild passerine bird. PeerJ 6:e5936. https://doi.org/10.7717/peerj.5936

Vágási CI, Pătraș L, Pap PL, et al (2018) Experimental increase in baseline corticosterone level reduces oxidative damage and enhances innate immune response. PLOS ONE 13:e0192701. https://doi.org/10.1371/journal.pone.0192701

Vágási CI, Vincze O, Pătraș L, et al (2019) Longevity and life history coevolve with oxidative stress in birds. Functional Ecology 33:152–161. https://doi.org/10.1111/1365-2435.13228

Manuscripts in preparation or submitted:

Bize P et al. Insulin-like growth factor 1 is related to adult body size and telomere lengths in alpine swifts. Manuscript in preparation.

Lendvai ÁZ et al. (a) The development of a radioimmunoassay for the measurement of avian IGF-1. Manuscript in preparation.

Lendvai ÁZ, et al. (b) Insulin-like growth factor 1 induces oxidative damage, but does not affect survival in bearded reedlings. Submitted manuscript.

Lendvai ÁZ et al. (c) Insulin-like growth factor 1 does not affect growth rate during natural molt. Manuscript in preparation.

Sirman A et al. (a) Natural variation of insulin-like growth factor-1 and telomere dynamics across multiple years in house sparrow nestlings. Manuscript in preparation.

Sirman A et al. (b) Manipulation of insulin-like growth factor-1 on nestling growth and telomere dynamics across years in house sparrow nestlings. Manuscript in preparation.

Salmon P et al. Growing up and old: are early-life IGF-1 levels associated with later-life cellular ageing? Manuscript in preparation.

Tablado Z et al. Coupling behaviour and physiology: is it possible in the context of stress reactivity? Submitted manuscript.

Tóth Z et al. The effects of nutritional stress on insulin-like growth factor 1 in bearded reedlings. Manuscript in preparation.

Valdebenito JO, Halimubieke N, Lendvai ÁZ, et al. Immunosuppression and the cost of reproduction in male birds. Manuscript in preparation.

Vágási CI, et al. (a) The Relationship between Hormones, Glucose and Oxidative Damage is Condition- and Stress-dependent in a Free-living Passerine Bird. Submitted manuscript.

Vágási CI, Fülöp A, Osváth G, et al. (b) Social Groups with Diverse Personalities Mitigate Physiological Stress. Submitted manuscript.

Conference presentations

(excluding presentations that have led to a publication)

Fülöp A et al. 2019. Diverse social groups are less stressful. Talk at the 19th European Ornithologist Union Meeting.

Salmon P et al. 2019. Growing up and old: are early-life IGF-1 levels associated with later-life cellular ageing? Talk at the 19th European Ornithologist Union Meeting.

Lendvai ÁZ. 2019. The role of the insulin-like growth factor 1 in the mediation of life history decisions in birds. Talk at the 19th European Ornithologist Union Meeting.

Tóth et al. 2019. Insulin-like growth factor-1 levels increase in response to food restriction in a passerine. Poster at the 19th European Ornithologist Union Meeting.