Final scientific report for OTKA Grants No. T046661 and No. NF61143*

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The main aim of the project was to investigate how internal state variables effect optimal behaviour in general, and the optimal timing of major life history events over the annual cycle, in particular. To accomplish this aim we developed a couple of annual routine models and performed various field observations and aviary experiments.

1. Theoretical work

1.1. Optimal moult strategies

Z. Barta, A. I. Houston, J. M. McNamara, R. K. Welham, A. Hedenström, T. P. Weber and O. Feró (2006) Annual routines of non-migratory birds: optimal moult strategies. **Oikos** 112: 580–593.

IF: 3.381

*Here I report on both grants because they supplemented each other: T046661 provided the material costs, while NF61143 gave the salaries.

In a periodically changing environment it is important for animals to properly time the major events of their life in order to maximise their lifetime fitness. For a non-migratory bird the timing of breeding and moult are thought to be the most crucial. We develop a state-dependent optimal annual routine model that incorporates explicit density dependence in the food supply. In the model the birds' decisions depend on the time of year, their energy reserves, breeding status, experience, and the quality of two types of feathers (outer and inner primaries). Our model predicts that, under a seasonal environment, feathers with large effects on flight ability, higher abrasion rate and lower energetic cost of moult should be moulted closer to the winter (i.e. later) than those with the opposite attributes. Therefore, we argue that the sequence of moult may be an adaptive response to the problem of optimal timing of moult of differing feathers within the same feather tract. The model also predicts that environmental seasonality greatly affects optimal annual routines. Under high seasonality birds breed first then immediately moult, whereas under low seasonality an alternation occurs between breeding and moulting some of the feathers in one year and having a complete moult but no breeding in the other year. Increasing food abundance has a similar effect.

1.2. Optimal moult strategies in migratory birds

Z. Barta, J. M. McNamara, A. I. Houston, T. P. Weber, A. Hedenstrom and O. Fero, (2008) Optimal moult strategies in migratory birds. **Philosofical Transactions of the Royal Society B** 363: 211–229.

IF: 4.579

Avian migration, which involves billions of birds flying vast distances, is known to influence all aspects of avian life. Here we investigate how birds fit moult into an annual cycle determined by the need to migrate. Large variation exists in moulting patterns in relation to migration: for instance, moult can occur after breeding in the summer or after arrival in the wintering quarters. Here we use an optimal annual routine model to investigate why this variation exists. The modelled bird's decisions depend on the time of year, its energy reserves, breeding status, experience, flight feather quality and location. Our results suggest that the temporal and spatial variations in food are an important influence on a migratory bird's annual cycle. Summer moult occurs when food has a high peak on the breeding site in the summer, but it is less seasonal elsewhere. Winter moult occurs if there is a short period of high food availability in summer and a strong winter peak at different locations (i.e. the food is very seasonal but in opposite phase on these areas). This finding might explain why only long-distance migrants have a winter moult.

1.3. Optimal immune defence

A. I. Houston, J. M. McNamara, Z. Barta and K. C. Klasing (2007) The effect of energy reserves and food availability on optimal immune defence. **Proceedings of the Royal Society B** 274: 2835–2842.

IF: 3.611

In order to avoid both starvation and disease, animals must allocate resources between energy reserves and immune defence. We investigate the optimal allocation. We find that animals with low reserves choose to allocate less to defence than animals with higher reserves because when reserves are low it is more important to increase reserves to reduce the risk of starvation in the future. In general, investment in immune defence increases monotonically with energy reserves. An exception is when the animal can reduce its probability of death from disease by reducing its foraging rate. In this case, allocation to immune defence can peak at intermediate reserves. When food changes over time, the optimal response depends on the frequency of changes. If the environment is relatively stable, animals forage most intensively when the food is scarce and invest more in immune defence when the food is abundant than when it is scarce. If the environment changes quickly, animals forage at low intensity when the food is scarce, but at high intensity when the food is abundant. As the rate of environmental change increases, immune defence becomes less dependent on food availability. We show that the strength of selection on reserve-dependent immune defence depends on how foraging intensity and immune defence determine the probability of death from disease.

1.4. Climate change and scheduling migration

A. Hedenström, Z. Barta, B. Helm, A. I. Houston, J. M. McNamara, N. Jonzén, (2007) Migration speed and scheduling of annual events by migrating birds in relation to climate change **Climate Research** 35: 79–91.

IF: 1.519

Empirical evidence for changed timing of migration in birds is emerging from both American and Euro-African migration systems. These changes are usually interpreted as a consequence of changes in climate. Responses in timing of migration and breeding may differ among species, and the adaptive significance is not well understood. There is a lack of theoretical understanding about time-shifts in life-history events due to climatic changes. In the present paper, we use 2 separate modelling approaches to investigate the effects of climate change on migration. We first use a simple model of flight speed and foraging to explore which factors may influence migration speed and stopover itinerary. Our second approach derives predictions based on an annual routine model, where behavioural strategies regarding timing of migration, breeding, moult and number of breeding attempts are modelled in an environment comprising 4 locations (breeding and wintering sites and 2 stopover sites). This approach takes account of interrelationships between behaviours and seasons as a step towards realistic modelling of migratory connectivity. Departure from the wintering site is advanced in relation to the advancement of spring if the moult is in summer, but not so for species with a winter moult, while arrival at the breeding site is advanced for both moult scenarios. Timing of breeding and number of successful broods were also affected by spring advancement, while start of moult is relatively unaffected by climate change. These optimal solutions under the modelled set of parameters are discussed with respect to current knowledge of the mechanisms underlying seasonal timing in birds.

1.5. The use of optimal annual routines in conservation biology

O. Fero, P. A. Stephens, Z. Barta, J. M. Mcnamara, and A. I. Houston, (2008) Optimal annual routines: new tools for conservation biology? **Ecological Applications** 18: 1563–1577.

IF: 3.571

Many applied problems in ecology and conservation require prediction, and population models are important tools for that purpose. Formerly, the majority of predictive population models were based on matrix models. As the limitations of classical matrix models have become clearer, the use of individual-based models has increased. These models use behavioral rules imposed at the level of the individual to establish the emergent consequences of those rules at the population level. Individual behaviors in such models use an array of different rule types, from empirically derived probabilities to long-term fitness considerations. There has been surprisingly little discussion of the strengths and weaknesses of these different rule types. Here, we consider different strategies for modeling individual behaviors, together with some problems associated with individual-based models. We propose a novel approach based on modeling optimal annual routines. Annual routines allow individual behaviors to be predicted over a whole annual cycle within the context of long-term fitness considerations. Temporal trade-offs between different behaviors are automatically included in annual routine models, overcoming some of the primary limitations of other individual-based models. Furthermore, as well as population predictions, individual behaviors and indices of condition are emergent features of annual routine models. We show that these can be more sensitive to environmental change than population size, offering alternative, repeatable metrics for monitoring population status. Annual routine models provide no panacea for the problems of data limitations in predictive population modeling. However, as a result of their ability to deal with life-history trade-offs, as well as their potential for relatively rapid and accurate validation and parameterization, we suggest that annual routine models have strong potential for predictive population modeling in applied conservation settings.

1.6. Effect of latitude on avian life histories

McNamara J.M., Z. Barta, M. Wikelski, A.I. Houston, 2008. A theoretical investigation of the effect of latitude on avian life histories. **American Naturalist** 172 331-345.

IF: 4.543

Tropical birds lay smaller clutches than birds breeding in temperate regions and care for their young for longer. We develop a model in which birds choose when and how often to breed and their clutch size, depending on their foraging ability and the food availability. The food supply is density dependent. Seasonal environments necessarily have a high food peak in summer; in winter, food levels drop below those characteristic of constant environments. A bird that cannot balance its energy needs during a week dies of starvation. If adult predation is negligible, birds in low seasonal environments are constrained by low food during breeding seasons, whereas birds in high seasonal environments die during the winter. Low food seasonality selects for small clutch sizes, long parental care times, greater age at first breeding, and high juvenile survival. The inclusion of adult predation has no major effect on any life-history variables. However, increased nest predation reduces clutch size. The same trends with seasonality are also found in a version of the model that includes a condition variable. Our results show that seasonal changes in food supply are sufficient to explain the observed trends in clutch size, care times, and age at first breeding.

1.7. Optimal annual immunity

Barta, Z., J. M. McNamara, A. I. Houston, (ms) Optimal immunity over the annual cycle in non-migratory birds.

Having an efficient immune system is considered to be highly beneficial in a world that teems with parasites. The maintenance of this system is, however, costly because it requires resources that could be used for other purposes. It is not obvious how a bird's optimal level of immunity should vary over the year. For instance, the need to invest resources in reproduction or moult might lower the optimal level of immune defence. On the other hand, a high level of defence might be a prerequisite for successful breeding and moulting. Here we present an optimal annual routine model of the behaviour of non-migratory birds to investigate the optimal level of immune defence over the annual cycle. In our model a bird s decisions depend on the time of year and a set of state variables including the bird s energy reserves, breeding status, experience, quality of the primary flight feathers and condition of the immune system. We incorporate explicit density dependence in the food supply. We use the model to investigate how the optimal level of immune defence should change over the year and how seasonality in the chance of parasite infection influences this optimal level and the annual behaviour.

2. Empirical work

2.1. Increase of feather quality during moult

Pap, P.L., Barta, Z., Tökölyi, J., Vágási, I.C. (2007). Increase of feather quality during moult: a possible implication of feather deformities in the evolution of partial moult in the great tit. **Journal of Avian Biology** 38: 471-478.

IF: 2.472

Here we investigate the change in feather quality during partial post-juvenile and complete post-breeding moult in great tit Parus major by measuring the change in the number of fault bars and feather holes on wing and tail feathers. Feathers grown during ontogeny usually are of lower quality than feathers grown following subsequent moults at independence. This is reflected by higher number of fault bars and feather holes on juveniles compared to adults. Fault bars are significantly more common on tail and proximal wing feathers than on the distal remiges, indicating a mechanism of adaptive allocation of stress induced abnormalities during ontogeny into the aerodynamically less important flight feathers. On the contrary, feather holes produced probably by chewing lice have a more uniform distribution on wing and tail feathers, which may reflect the inability of birds to control their distribution, or the weak natural selection imposed by them. The adaptive value of the differential allocation of fault bar between groups of feathers seems to be supported by the significantly higher recapture probability of those juvenile great tits which have fewer fault bars at fledging on the aerodynamically most important primaries, but not on other groups of flight feathers. The selection imposed by feather holes seems to be smaller, since except for the positive association between hatching date, brood size and the number of feather holes at fledging, great tits' survival was not affected by the number of feather holes. During post-juvenile moult, the intensity of fault bars drops significantly through the replacement of tail feathers and tertials, resulting in disproportional reduction of the total number of fault bars on flight feathers related to the number of feathers replaced. The reduction in the number of fault bars during post-juvenile moult associated with their adaptive allocation to proximal wing feathers and rectrices may explain the evolution of partial post-juvenile moult in the great tit, since the quality of flight feathers can be increased significantly at a relatively small cost. Our results may explain the widespread phenomenon of partial post-juvenile moult of flight feathers among Palearctic passerines. During the next complete post-breeding moult, the total number of fault bars on flight feathers has remained unchanged, indicating the effectiveness of partial post-juvenile moult in reducing the number of adaptively allocated fault bars. The number of feather holes has also decreased on groups of feathers replaced during partial post-juvenile moult, but the reduction is proportional with the number of feathers moulted. In line with this observation, the number of feather holes is further reduced during post-breeding moult on primaries and secondaries, resulting in an increase in feather quality of adult great tits.

2.2. Diet quality affects post-nuptial molt and feather quality

Pap, P.L., Vágási, I.C., Czirják, G.Á., Barta, Z. (2008). Diet quality affects post-nuptial molt and feather quality of the house sparrow (Passer domesticus): interaction with humoral immune function? **Canadian Journal of Zoology** 86: 834-842.

IF: 1.493

We investigate the effects of nutritional limitation, humoral immune activation and their interaction on post-nuptial molt of aviary-kept house sparrows (Passer domesticus L., 1758). To do so, in a 2×2 experimental design we measured the progress of molt and the quality of feathers produced during molt in experimental groups of different diet quality (high and low) and humoral immune activation with sheep red blood cells (SRBC). Food quality, but not the activation of humoral immunity affected significantly the body mass and the process of molt. Sparrows feeding on low-quality food had decreased body mass and longer molt than the high-quality group. Low food quality, but not the activation of humoral immunity reduced significantly the length and weight (i.e. the quality) of primaries grown during molt. Birds responded significantly to injection with SRBC compared to the control group, but, the immune response was similar between nutritional groups. The absence of a negative effect of humoral immunity on molt in house sparrows might be related to the low energy and nutrition requirement of mounting and maintaining a humoral immune response.

2.3. The role of moult and feather abrasion in seasonal colour change

Tökölyi, J., Bókony, V., Barta, Z., (2008) Seasonal colour change by moult or by the abrasion of feather tips: a comparative study. **Biological Journal of the Linnean Society** 94: 711–721. **IF: 2.368**

Many birds undergo seasonal changes in plumage coloration by prebreeding moult, abrasion of cryptic feather tips, or both. Seasonal dichromatism is thought to result from optimizing coloration to the conflicting demands of different life-cycle periods, sexual selection for conspicuousness being substantial during the mating season, whereas selection for camouflage and for social signals may act in all seasons. Furthermore, energetic and time demands may constrain the extent of moult, thereby limiting colour change. We investigated the relative importance of several factors in shaping this variation in a songbird clade using phylogenetic comparative methods. We found that prebreeding moult relates most strongly to breeding onset and winter diet, demonstrating that both time and food availability constrain feather replacement. Feather abrasion was best predicted by winter flocking behaviour, and secondarily by open habitats, implying that exposure to predators and the simultaneous need for social signalling may favour the expression of partially obscured ornaments in the non-breeding season. The combined occurrence of prebreeding moult and feather abrasion was associated with the polygynous mating system, suggesting that species under strong sexual selection may employ both strategies of colour change to ensure the full expression of breeding coloration.

2.4. Life history predicts response to climate change

Végvári Zs., Bókony V., Barta Z., Kovács G. (in press) Life history predicts advancement of avian spring migration in response to climate change. **Global Change Biology**.
IF: 4.786

An increasing number of studies demonstrate that plant and animal phenologies such as the timing of bird migration have been advancing over the globe, likely as a result of climate change. Even closely related species differ in their phenological responses, and the sources of this variation are poorly established. We used a large, standardized dataset of first arrival dates (FAD) of migratory birds to test the effects of phylogenetic relationships and various life-history and ecological traits on the degree to which different species adapt to climate change by earlier migration in spring. Using the phylogenetic comparative method, we found that the advancement of FAD was greater in species with more generalized diet, shorter migration distance, more broods per year, and less extensive prebreeding molt. In turn, we found little evidence that FAD trends were influenced by competition for mating (polygamy or extra-pair paternity) and breeding opportunities (cavity nests). Our findings were robust to several potentially confounding effects. These evolutionary correlations, coupled with the low levels of phylogenetic dependence we found, indicate that avian migration phenology adapts to climate change as a species-specific response. Our results suggest that the degree of this response is fundamentally shaped by constraints and selection pressures of the species' life history, and less so by the intensity of sexual selection.

2.5. Causes and consequences of variation in feather quality

Vágási, I.C., Pap, P.L., Tökölyi, J., Székely, E., Barta, Z. (submitted). Causes and consequences of variation in feather quality in the great tit Parus major. Submitted to **Journal of Avian Biology**

One of the most important functions of moult is the renewal of old feathers, as deterioration due to wear and tear may impair flight performance leading to decreased fitness. The gradual shortening of the wing length due to abrasion during the period between two moult events is a well known phenomenon among birds, however, little is known about the factors responsible for feather degradation and its fitness consequences. Similarly, the source of variation and consequences of feather hole incidence has rarely been investigated. Here, we report results variation feather wear, feather holes and feather quality based on a three-year study on a great tit (Parus major L., 1758) breeding population. We found that season, age, sex (only during the breeding season), several physical condition parameters and the presence of feather holes are the main sources of variation in wear score. Feather deterioration was faster during the breeding related to the non-breeding season, which can be explained by the high workload of birds during reproduction. The increased feather abrasion of juveniles and females related to adults and males, respectively, may arise because of the juveniles' inferior feather quality compared to adults, and by the high female investment in parental duties related to males. Feather wear did not correlate with laying date, clutch and brood size. Juveniles and individuals in poor physical condition characterized through feather quality variables (thin rachis, low barbule density, fault-bars present) and large clutch and brood size had higher feather hole load related to adults and birds with superior quality, respectively. These results brings evidences that feather deformities are positively interrelated and can be used as reliable measures of feather quality and physical condition. We also discuss possible alternative explanations for the causes of feather holes, beside the widespread view that holes are feeding marks of chewing lice.

2.6. Seasonal changes in immune functions

Pap, P.L., Czirják, G.Á., Vágási, C.I., Barta, Z., Hasselquist, D. (submitted). Seasonal changes in immune functions differ between the sexes in house sparrows. Submitted to **Functional Ecology**

1. Seasonality in immune functions of wild-living animals is increasingly recognized as an adaptation to changing environmental conditions, reflecting the actual constraints between an effective defence against periodically emerging diseases and the sex specific cost of maintaining an effective immune function. Despite of the high complexity of the immune system, studies on immunoecology generally characterize the immune system through a few variables, however because the function differ among immune branches, we expect divergent responses of immune components to environmental seasonality.

2. We measured all major components of the immune system (innate, acquired, cellular, humoral) during the summer, autumn, winter and spring of male and female house sparrows Passer domesticus.

3. We found, that six out of the eight immune variables measured (bacteria killing capacity to limit E. coli or S. aureus infections, levels of the natural antibodies and complement, antibody response to keyhole limpet hemocyanin (KLH) and sheep red blood cells, T-cell memory swelling to KLH and to phytohemagglutinin) varied significantly among seasons.

4. The difference in immune response between the sexes was significant in five immune variables during the spring, when females had stronger immune function than males, while no variable varied with sex during the rest of the seasons. Immune function was related to the bib size of male house sparrows in one out of the eight immune variables, however, the relationship between T-cell memory swelling to KLH and bib size was significantly negative only during the summer.

5. Immune variables characterizing similar components of the immune system were positively correlated, indicating that through measuring one of these immune variables we can characterize a certain component of the immune system.

6. Our results show that the immune system is highly variable between seasons, probably as a result of the different environmental and social conditions, and that the sexes show different patterns over the annual cycle.

2.7. Carotenoids modulate the effects of coccidian infection

Pap, P.L., Vágási, I.C., Czirják, G.Á., Titilincu, A., Pintea, A., Barta, Z. (ms). Carotenoids modulate the effect of coccidian infection on moulting and immune response in a passerine bird.

Coccidiosis may have a serious effect on the fitness, reducing the availability of carotenoids important for physiological homeostasis and immune defense during stressful periods of the host. Avian moult is one of the most costly life history traits, and contrary to reproduction, the impairment in moulting may have at least one-year long lasting negative effect on the host. One could expect that the negative effect of parasitism on condition and moulting is modulated by the availability of carotenoids. Here, we manipulated both coccidian parasitism and availability of carotenoids in male aviary house sparrows (Passer domesticus) in a full factorial 2×2 experimental design and tested whether unrestricted access to carotenoids reduced the cost of parasitism in terms of condition, moulting and immune responses. We found that coccidians have a significant but transient negative effect on body mass which can be reduced if birds have access to carotenoid supplementation in the diet. Coccidian infestation, measured before moulting was significantly negatively related with moulting duration in the experimentally infested and non-supplemented birds, however the negative effect of parasites disappeared in carotenoid supplemented and infested, and in the medicated groups. Supplementation increased the plasma carotenoid concentration in both infested and medicated birds following infestation, however, after two months exposure to parasites plasma carotenoid concentration was highest in the carotenoid supplemented and medicated group, while no difference was observed between the non-supplemented medicated and infested groups. Within the experimentally infested groups birds with carotenoid supplemented food had an increased antibody response to sheep red blood cells (SRBCs), but not phytohemagglutinin induced swelling, related to non-supplemented birds. We found no impact of carotenoid supplementation on the immune function of birds from the medicated groups, suggesting that the imunostimulant effect of these pigments acts only under parasite pressure when the immune system is stimulated. The positive correlation between coccidian infestation and the strength of the humoral immune response against SRBC in non-supplemented and infested group indicates that this part of the immune system play an important role in defense against this parasites. Carotenoids may modulate the effect of coccidian infestation on immune defense, as within infected and supplemented group no relationship was found between parasitism and antibody titre. Our results indicate that carotenoids may modulate the fitness consequences of parasitism on moulting, a life history trait largely neglected in animal ecology studies.

2.8. Moulting speed affects feather quality and plumage ornamentation

Vágási, C.I., Pap, P.L., Barta, Z. (ms). Moulting speed affects feather quality and plumage ornamentation in the house sparrow (Passer domesticus)

Among birds an impressive diversity of pigment-based plumage signals convey information to receivers in sexual and/or social context. These ought to incur considerable production or maintenance costs to be reliable, thus to be maintained by selection. If a production cost exits this should act during the development of that particular plumage trait. Thus receivers have to rely on information transmitted for roughly a one-year-period that refers to the condition of the signaller in the preceding moulting period. Here, we studied experimentally a hypothesis predicting that birds entering relatively later the moulting period should moult faster which compromises the elaborateness of ornamental plumage traits. We manipulated the photoperiod in indoor aviaries, with one group (control) of adult male house sparrows (Passer domesticus) being held under natural-like photoperiod, while the other (experimental) under an accelerated photoperiod. The photoperiod manipulation affected both the flight feather quality and the plumage signals. Namely, sparrows moulting faster in the experimental group grew lighter and shorter primaries, and had a smaller black throat patch (bib) area and reduced brightness of the white wing-bar. We could not found any effect on bib brightness and wing-bar area. Our results indicate that plumage signals may not only convey information about the condition of the signaller during moult but they might also integrate information on a longer period before moult. We discuss the possible outcomes of shedding feathers in a relatively reduced time window from a life-history and social selection perspective.