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"Effects of environmental stochasticity on optimal timing of annual behaviour"

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1 Introduction

Our aim was to understand the effects of year-to-year environmental stochasticity on the temporal organisation of the annual cycles of living creatures. We planned to accomplish this aim by the following:

- developing an annual routine model of environmental stochasticity;
- with this model:
  - investigating gonad size development and breeding decisions in birds;
  - studying moult in tropical birds;
  - understanding differences between urban and rural life histories;
- implementing a model to understand use of cues as an adaptation to environmental stochasticity; and
- using neural nets to study control mechanisms allowing animals to cope stochasticity.

2 Results

2.1 Models

We have a developed a representation of environmental stochasticity within the framework of annual routines. The details of the model can be found in Tökölyi et al. (2011) and Tökölyi (2011). With the model we obtained the following results.

Organisms living in periodically changing environments adjust their life history events to the changes in food availability. When these changes are not entirely predictable animals face a trade-off between maintaining physiological preparedness (which can be costly) and being unprepared (which decreases the chances of successful reproduction). To investigate this problem, we developed an optimal annual routine model of gonad regulation in birds. Most birds regress their reproductive organs during non-breeding periods, but to start breeding again they need to have functional gonads. Maintaining the gonads in this state is costly, but because it takes time to achieve this state, if gonads are not functional the bird may be unable to exploit a possible breeding opportunity. We explore the resolution of this trade-off in environments where favorable periods can occur at any time of the year and variability in the length of good and bad periods can be altered. Consistent with empirical studies of reproductive behavior in unpredictable environments, we find that birds maintain the gonads partially activated during unfavorable conditions in many cases. However, gonad regulation may differ strikingly depending on the consistency of the good and bad periods. Furthermore, seasonal changes in food availability lead to the entrainment of reproduction and the segregation of the breeding and non-breeding season, even if the magnitude of seasonality is small compared to the degree of environmental fluctuations. These results indicate that several aspects of the environment need to be taken into account to understand reproductive behavior in unpredictable environments. Given that the trade-off between the costs and benefits of maintaining physiological preparedness is not limited to birds, our results have implications for understanding behavioral exibility in other organisms as well (Tökölyi et al., 2011).

Behavioral exibility enables animals to adjust their life history decisions to unpredictable events thereby increasing reproductive success and population persistence in variable environments. However, to attain exibility, the animals have to stay prepared, which can be costly. This costliness of plasticity can ultimately constrain the animals ability to respond to environmental changes, such as the advancement of spring due to recent changes in global climate. Here, we analyze a model of avian annual routines to find the optimal levels of reproductive readiness in seasonal environments. Our results indicate that

exibility is generally higher in environments with pronounced year-to-year variability in the onset of spring if food availability during summer is uniform. When there is a peak in food availability during mid-summer, reproduction becomes entrained to this peak and reproductive exibility is low under most conditions. Thus, the response of birds to sudden changes in the environment is constrained in low-variability environments, but also in environments with high year-to-year variability in the onset of spring if the peak of food availability is stable. Birds that cannot repond to the earlier onset of spring by advancing their breeding season suffer a decrease in reproductive success, but this decrease is not same in birds showing the same degree of phenological response; birds in highly seasonal environment in general suffer a much higher decrease in reproductive success (Tökölyi, 2011).

Organisms time activities by using environmental cues to forecast the future availability of important resources. Presently, there is limited understanding of the relationships between cues and optimal timing, and especially about how this relationship will be affected by environmental changes. We develop a general model to explore the relation between a cue and the optimal timing of an important life history activity. The model quanties the fitness loss for organisms failing to time behaviours optimally. We decompose the immediate change in fitness resulting from environmental changes into a component that is due to changes in the predictive power of the cue and a component that derives from the mismatch of the old response to the cue to the new environmental conditions. Our results show that consequences may range from negative, neutral to positive and are highly dependent on how cue and optimal timing and their relation are specically affected by environmental changes (McNamara et al., 2011).

2.2 Comparative studies

We also investigate factors determining annual behaviour by the aids of comparative analyses.

The breeding season of long-distance migratory birds often starts later and is shorter than in resident or short-distance species breeding at the same latitude, but the reason for this is unclear. Here we investigate the association between migration distance and breeding phenology in a group of passerine birds, the finches and their allies, using phylogenetic comparative methods. We confirm that migration distance is related to aspects of the species breeding phenology after controlling for the effect of potentially confounding variables. Directional phylogenetic analyses suggest that evolutionary transitions in migration distance are determined by the breeding phenology. A relatively long migration distance is more likely to evolve in birds with a late, short breeding season, whereas transitions to short distance migration are more likely to occur in lineages with an early, long breeding season. These results suggest that migration

distance is constrained by breeding phenology and not vice versa. Thus, breeding phenology may be an important ultimate factor shaping the evolution of migratory strategies (Tökölyi and Barta, 2011).

Mammals display considerable geographic variation in life history traits. To understand how climatic factors might influence this variation, we analysed the relationship between life history traits - adult body size, litter size, number of litters per year, gestation length, neonate body mass, weaning age and age at sexual maturity - and several environmental variables quantifying the seasonality and predictability of temperature and precipitation across the distribution range of five terrestrial mammal groups. Environmental factors correlated strongly with each other, therefore, we used principal components analysis to obtain orthogonal climatic predictors that could be used in multivariate models. We found that in bats, primates and even-toed ungulates adult body size tends to be larger in species inhabiting cold, dry, seasonal environments, whereas in carnivores and rodents a smaller body size is characteristic of warm, dry environments, suggesting that low food availability might limit adult size. Species inhabiting cold, dry, seasonal habitats have fewer, larger litters and shorter gestation periods; however, annual fecundity in these species is not higher, implying that the large litter size of mammals living at high latitudes is probably a consequence of time constraints imposed by strong seasonality. On the other hand, the number of litters per year and annual fecundity were greater in species inhabiting environments with higher seasonality in precipitation. Lastly, we found little evidence for specific effects of environmental variability. Our results highlight the complex effects of environmental factors in the evolution of life history traits in mammals (Tökölyi et al., 2014).

Herbarium collections contain long-term data for a wide range of taxa and provide unique opportunities to evaluate the importance of life-history components in driving species-specific responses to climate change. Here, we analysed the relationships between change in flowering dates and life-history traits within a phylogenetic framework. The study is based on an extensive data set of herbarium specimens of orchids collected in Hungary between 1837 and 2009, supplemented by recent field observations (1980-2011). Of the 39 taxa investigated, 31 (79%) showed apparent advancement in mean flowering time. Among these, advancement was statistically significant in nine taxa. The rest (eight taxa) showed non-significant delays in flowering. Averaging across all taxa, flowering time advanced by 3 days (3.8% of flowering period) during the last 50 years compared with the period before 1960. In taxa showing significant advancement, flowering times advanced by 7.7 days (8.6% of the flowering per- iod). The most extreme advancement was 13.9 days. Multivariate models were used to evaluate ways in which life history may affect phenological responses to climate change. Pollination mode (i.e. deceptive vs.

rewarding vs. autogamous), life span (i.e. short-lived vs. long-lived), biogeographical distribution type (i.e. Mediterranean vs. non-Mediterranean) and flowering time (i.e. mean date of blooming) emerged as important factors that influence changes in flowering through time. Phylogenetic relatedness did not predict phenological response. The strongest response was observed in orchids that flower relatively early in spring, exhibit an autogamous or deceptive pollination mechanism, have a long life span and possess a Mediterranean centre of distribution. Our investigation demonstrates that the majority of Hungarian orchids have shifted their yearly mean flowering to earlier dates during the past 50 years. Certain life-history traits, but not phylogenetic relatedness, were found to be important in predicting climatic responsiveness in European terrestrial orchids (Molnár et al., 2012).

2.3 Field studies

The seasonal change, i.e. the marked differences between seasons of low and high productivity, in the abundance of ectosymbionts and the defence intensity of the host against pathogens is a well defined characteristic of temperate zone organisms. Here we investigated the seasonal variation in the uropygial gland size and the abundance of Proctophyllodes feather mites on the wing feathers of house sparrows Passer domesticus in two breeding populations. The size of the uropygial gland varied significantly in male and female house sparrows over the annual cycle. The gland was small during the non-breeding and mating season, after that it started to grow sharply, reaching its maximum size during breeding. Females had larger gland volumes than males during breeding, and the increase in gland size during breeding was more pronounced in females than in males. The number of feather mites was the lowest during breeding, followed by an increase during moult and reaching its maximum between the wintering and mating seasons. The absence of a significant relationship between the uropygial gland size and the abundance of feather mites, after controlling for potential confounding variables, supports the view that gland oils do not regulate the number of mites. To investigate further this hypothesis, through a full factorial experimental design we tested the effect of uropygial gland and photoperiod manipulation on the population size and population dynamics of feather mites. The manipulation of uropygial gland had no effect on mites, supporting our observational results. As a result of the experimentally increased day-length, the abundance of feather mites on wing feathers decreased significantly and more sharply than in the control group, supporting the previous anecdotal evidence about the photosensitivity of these organisms. Using photoperiodic cues, feather mites may respond to seasonal changes that affect their life-history and population dynamics (Pap et al., 2010).

The trade-off between current and residual reproductive values is central to life history theory, although the possible mechanisms underlying this trade-off are largely unknown. The 'molt constraint' hypothesis suggests that molt and plumage functionality are compromised by the preceding breeding event, yet this candidate mechanism remains insufficiently explored. The seasonal change in photoperiod was manipulated to accelerate the molt rate. This treatment simulates the case of naturally late-breeding birds. House sparrows Passer domesticus experiencing accelerated molt developed shorter flight feathers with more fault bars and body feathers with supposedly lower insulation capacity (i.e. shorter, smaller, with a higher barbule density and fewer plumulaceous barbs). However, the wing, tail and primary feather lengths were shorter in fast-molting birds if they had an inferior body condition, which has been largely overlooked in previous studies. The rachis width of flight feathers was not affected by the treatment, but it was still condition-dependent. This study shows that sedentary birds might face evolutionary costs because of the molt rate feather quality conflict. This is the first study to experimentally demonstrate that (1) molt rate affects several aspects of body feathers as well as flight feathers and (2) the costly effects of rapid molt are condition-specific. We conclude that molt rate and its association with feather quality might be a major mediator of life history trade-offs. Our findings also suggest a novel advantage of early breeding, i.e. the facilitation of slower molt and the condition-dependent regulation of feather growth (Vágási et al., 2012).

3 Deviations

We are still working on the urban-rural model. At the moment we finalise the model specification. It turns out during the project that the differences are rather numerous between urban and rural life and it is far from trivial to develop an annual routine model which are capable to characterise most of these differences. This explains the delay. The key aspect of the developing model is size which seems a key differences between urban and rural birds. We expect the first result from this model at the end of 2014.

The model of tropical moult turned out to be much more complicated than we expected at the planning of the project. Given this complication we decided to drop this line of investigation as pursuading further it would be less fruitful.

We have to abandon the neural network model of annual routine control mechanism, because we cannot get a converging solution.

Nevertheless we also accomplished many other investigations not listed in the plan (see above).

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