UNIWERSYTET IM. ADAMA MICKIEWICZA W POZNANIU
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Review of the PhD Thesis "Macroecology and macroevolution of birdsong" by Peter Mikula

I have received for review PhD Thesis entitled "Macroecology and macroevolution of birdsong" in a form of so-called cumulative work consisting of four contributions comprising two published papers, one submitted manuscript under review and one unsubmitted manuscript. The thesis contains also Abstract and general Introduction chapter, as well as a set of declarations about contribution to particular manuscript from the author Peter Mikula and his supervisor prof. Tomáš Albrecht.

The PhD thesis I evaluated is placed in one of the mainstreams of behavioural ecology in terms of methodology. This is a comparative study aimed at finding evolutionary trajectories of one of the most important sexually selected avian trait, namely song. Peter Mikula limited his work to passerines, but the word 'limited' should be treated here as euphemism. The first impression I had during my reading was the admiration for the great material the student managed to grasp and compile. Before going into details, I briefly mention the contents of particular parts to which I will later refer as to Chapters from 1 to 4.

I suppose that the first, still unpublished Chapter 1, is the most important part of the whole work. Peter Mikula has focused in it on identifying factors affecting song complexity among nearly five thousands passerine species with the use of a proposed single metric of this song characteristic. Chapter 2 explores whether correlations exist between traditionally used song complexity metrics based on between- and within-song diversity of unique syllables and a novel frequency-derived metric used at a wider scale study by another author. This chapter is a published paper being a critical commentary to publication of Pearse et al. (2018) from *Evolution*. Chapter 3 is similar to the first one, but here Peter Mikula aimed to identify the ecological and evolutionary underpinnings of song frequency variation among over five thousands passerine species. Finally, Chapter 4 limits range of analysed units to 269 bird species from S Africa, but raises very ambitious questions about environmental and social factors affecting evolution and variability of duetting and female solo song.

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Comments to Chapter 1

Mikula, P., Valcu, P., Brumm, H., Blažková, B., Bulla, B., Dale, J., Forstmeier, W., Petrusková, T., Kempenaers, B. & Albrecht. T. Global variation in birdsong complexity is best explained by environmental variability. (unsubmitted manuscript)

Bird song is one of the most variable and multidimensional sexually selected trait. During last ~70 years an increasing number of research on bird song revealed dozen of patterns how song may vary between- and within-species, and how different informative value it may have. One of the song dimensions which attracted researchers the most was always complexity, likely because it is sometimes simply astonishing. It is really hard to listen to song of - for example - a grasshopper warbler and a nightingale and do not ask, why they are so divergent? Paper presented in Chapter 1 is an attempt to answer this question with help of a single song complexity metrics used. The complexity of birds song could be measured in many different ways and it is not possible, in my opinion, to give a single metrics which reflect everything at one time. However, acoustic waves when used by animals as signals have one common character of each wave. They change in time. Mikula and co-authors proposed a simple metrics which grasps this feature by presenting how many different elements are presented by a bird within a 50-element sequence of song. Such approach has many advantages and I believe that it is a good compromise for measuring so called repertoire variation among species within reasonable time and allowing for conclusive between species comparisons. The analysis is based on data coming from 4,939 passerines from Oscines and Suboscines clades. As I have written earlier, interspecific comparison is a classic of behavioural ecology approach but here we have a classic in a contemporary edition with a phylogenetically informed analyses. The results are to some extent surprising as authors found out that despite finding several interesting associations between song complexity and life-history traits and environment characteristics... most of them disappeared after adding phylogenetical information. What they found left is a positive correlation between song complexity and habitat generalism of species.

The result of such large comparisons by definition presents some trends, associations between traits or, in some case, big divisions reflecting critical adaptations. The adaptation to song learning in birds could be considered such one. The character of such approach does not allow to focus on some details. I just wanted to point out that the general picture presented by Mikula does not exclude existence of some strong relations between song complexity and analysed traits or environmental condition in some phylogenetically distinct group or species living in a very specific conditions.

I have a few technical objections to methods and interpretation of some data in this part. For example, (1) to assigning some non-monogamous species to this group in analysis; (2) What is exactly meant by "Song repertoire size" in Table S1?; or (3) Why living in variable environment may result in more intensive competition for mates and resources?

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Comments to Chapter 2

Mikula, P., Petrusková, T. & Albrecht, T. 2018. Song complexity – no correlation between standard deviation of frequency and traditionally used song complexity metrics in passerines: A comment on Pearse et al. (2018). *Evolution* 72: 2832–2835.

The Chapter 2 is a commentary paper discussing the use of a specific song complexity metrics presented in an earlier study by Pearse et al. (*Evolution* 72: 944-960) and used for studying macroevolution of bird song. Mikula raised in this paper questions about meaning of this new metric (called SD of frequency or SDF) - and relationships between it and other metrics used in the past. As he has noticed, the SDF in some cases gives counterintuitive values and species known as very complex in their song behaviour seem to be less complex. For example, the mentioned by me earlier species from *Locustella* and *Luscinia* genus are such a case. This is a very useful part of Mikula's PhD thesis and is very up-to-date, allowing for better interpretation of Pearse and colleague work. I agree with most of Mikula's arguments and especially, I find out doing a large scale species comparison with not very well tested indices a potentially misleading.

Comments to Chapter 3

Mikula, P., Valcu, M., Brumm, H., Bulla, M., Forstmeier, W., Petrusková, T., Kempenaers, B. & Albrecht, T. A global analysis of song frequency in passerines provides no support for the acoustic adaptation hypothesis but suggests a role for sexual selection. (under review)

In the Chapter 3, Mikula and co-authors took for the analysis the next important bird song feature, namely frequency. Differently than in case of song complexity in Chapter 1, they were more focused here on direct testing predictions resulting from some hypotheses (acoustic adaptation h., morphological adaptation h., sexual selection h.). Again, with the use of a large multispecies dataset and well-tuned, phylogenetically informed approach, they tested whether lower-frequency songs are associated with (1) more closed (forested) habitats, (2) larger body size and (3) stronger male-biased sexual size dimorphism. The results obtained are very interesting and to some extent contradictory to the earlier findings. Mikula indicated that song frequency decrease with increasing body mass and size of male-biased dimorphism, what was expected. However, there was no support for the acoustic adaptation hypothesis. I found this result interesting but controversial, and for me it could be a new start of the story how environment affect songs, rather than the end. Firstly, based on the past studies I am rather convinced that song evolved under many factors acting and multi-species comparisons are only giving some general weights, or average importance of each of the factor taken into account. Hence, finding support for the body size effect does not mean that habitat is not important and vice versa. However, I am inclined to admit that the phylogeny primarily affects the extent of trait variability, which could be later tuned by sexual selection or/and environment. In some special cases, the phylogeny effect may also disappear, for example when a new adaptation allow a going down with song frequency as in species having elongated tracheas or air sacks. However, my biggest concern is

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related to the way how habitat density was measured. I fully understand, that for a such big scale comparison authors had to use some index or few indices of habitat density and the one they have chosen (tree cover) is not the bad one. I just suggest, that this weak point should be taken seriously into account in results interpretation. For example, a dense forest would probably receive a maximum value of tree cover index. However, a bird species which are living in such forest may be specialised for living in many different micro-habitats which may dramatically differ in sound propagation characteristics. Species spending all time on the ground are faced with completely different transmission problems than those who live in canopy or are flexible in their choice of song posts. All this huge variation is for simplicity hidden under two variables: tree cover and habitat type. That is probably too small for catching relations which in my opinion exist and which were shown many times in several small scale studies, also cited by Peter Mikula in his thesis. I think that further comparison limited to a smaller but carefully chosen and better known (by meaning of song behaviour ecology) species would be very fruitful.

I have a few technical remarks to this part. For a hard to understand reasond authors did measured sound frequency with two different resolutions resulting from the choice of FFT parameters in Raven Pro. These resulted in a biased accuracy of measurement (172 or 21.5 Hz) within the dataset and was completely unnecessary as do not demanded more work. The pattern obtained for species from NE Africa looks indeed very strange, and as noticed authors it demands careful interpretation or maybe even reanalysis (e.g. checking if all condition of data selection were fulfilled).

Instead of calling for more large-scale empirical studies on acoustic signal frequency in other animal groups as independent replication studies, I would rather suggest detailed studies on species with better known ecology of signalling allowing of better placement of the species in its acoustic environment.

Comments to Chapter 4

Mikula, P., Tószögyová, A., Hořák, D., Petrusková, T., Storch, D. & Albrecht, T. 2020. Female solo song and duetting are associated with different levels of territoriality in songbirds. *Behavioural Ecology* 31: 322–329.

I really like the last Chapter 4 of Peter Mikula PhD thesis. The candidate used South African birds assemblage as a model group for finding association between territoriality and both duetting and female solos singing. The choice of this avian group was very good as Bottom of Africa comprises tropical or subtropical region, diversified habitats and many phylogenetically divergent duetters and female singing species. In this already published paper, Mikula and co-authors found out that the primary driver of the evolution of female solo song and duetting in S Africa birds is territoriality. These results fits and complement a few other recent studied considering female song evolution (e.g. Odom et al. 2014, *Nature Communications* 5:3379) and it seems that thanks to the Mikula's paper we have better and better picture of bird song evolution in context of duetting and female solo.

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Summarizing and conclusions

All the remarks I have made to the thesis have nature of valuable (at least for me) discussion on the interpretation of the results. They do not call into question the validity of the objectives of the work or its methodology. I believe that Peter Mikula work gives a good contemporary background for in depth analysis of song evolution and ecology and is indicating some new, promising directions. To conclude, I declare that the thesis submitted by Peter Mikula, entitled "Macroecology and macroevolution of birdsong" illustrates his ability to carry out independent scientific research of high quality according to the law requirements on academic titles and degrees. Therefore, I fully support the application of Peter Mikula for obtaining relevant academic degree.

Yours sincerely,

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