

**Oponent's review of Doctoral dissertation thesis by Mgr. Peter Mikula
'MACROECOLOGY AND MACROEVOLUTION OF BIRDSONG'
in the field of Zoology, Faculty of Science, Charles University Prague**

In his dissertation, Peter Mikula focuses on a very interesting topic. Songs of passerines have received previously a vast amount of attention from researchers and this dissertation significantly expands and complements the existing knowledge. This is mainly because the author does not focus only on more common research typically involving only a few bird species, but includes a very detailed global synthesis covering almost the entire global species diversity of passerines, the largest avian clade. Because many factors are at play and may affect the character of bird song, the decision to address this topic on a global scale was desirable.

The thesis is well structured. It consists of four chapters, preceded by a legibly written introduction. The following are two published papers, one submitted manuscript, and one manuscript in preparation.

The 'Introduction' is elaborated at a high scientific but very comprehensible level. I really appreciate this brief introduction based on an extensive body of literature, which confirms author's excellent erudition in the studied topics. The chapter goes through an interesting history of the study of bird singing but it also covers other important topics such as how to define song complexity, fundamental metrics for comparative research. At the end of this chapter, I somewhat missed any short but clear conclusion that would emphasize the importance of the author's key findings and would outline potential interpretation risks and research challenges for future work.

The four following chapters correspond to the manuscripts or published papers, with Peter being the first author in all of them, always with a team of collaborators. There are resounding names from the Max Planck Institute for Ornithology, Germany, as well as from his home institution. The contributions of all co-authors are correctly specified. The attached studies include two papers published in highly ranked journals *Evolution* and *Behavioral Ecology*, one manuscript under review and one attached as a manuscript in preparation.

The study on song complexity is published as a technical comment in *Evolution* and questions the current claim that the standard deviation of song frequency can be used as a surrogate for song complexity, even though the authors agree that some simple metrics describing birdsong complexity is needed for comparative analysis of highly variable birdsong on large-scales. This only proves how difficult it is to find such a surrogate indicator. I like this paper and consider it a great critical point for the global comparative study (included as the manuscript of Chapter 1). The second published paper deals with solo song and duetting of passerine females in South Africa. The authors showed that both solo song and duetting are associated with a higher level of territoriality and long-term social bonds, but not directly with cooperative breeding, as indicated previously by some authors. Does this mean that the previous studies have been targeted too locally and their results misinterpret the real state? Would it be possible to repeat the analysis elsewhere in the world on other passerines with cooperative breeding not so clearly correlated with high territoriality and long-term social bonds? I wonder also if it is common that male and female songs differ to the extent that the sex of the singing bird can be reliably determined by conspecifics.

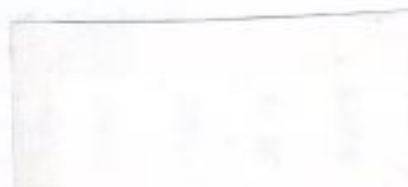
A study representing Chapter 3 (under review) provides critical insight into the general validity of the acoustic adaptation hypothesis. This is an original and very valuable study working with world databases of bird voices. Instead of the acoustic adaptation hypothesis, the results of a thorough analysis reveal that the evolution of peak song frequency in passerines is primarily controlled by

morphological constraints and is associated with sexual size dimorphism. However, the effect sizes were small, explaining 1–12% of the variation, which means that they are probably not fundamental drivers of the measured song characteristic. Given the little explained variation, can you suggest yet another factor that could be crucial in shaping the peak song frequency (although we may not be able to estimate it with the currently available data)? Would it be possible to replace the peak song frequency with another interesting bird song traits? How about other song frequency estimates, such as the minimum song frequency, song frequency range etc.? If song frequency represents a honest and costly signal in some species where it plays a role in sexual selection, I wonder whether we can expect greater variability in this trait within populations. Are there studies that address this issue in detail? Finally, how would you explain the seeming discrepancy between your finding based on the analysis involving almost all passerine species, and the previous studies dealing with smaller subsets of species? Is this discrepancy mostly due to a type I error, some statistical fishing or does it work for some groups while it cannot be applied globally?

Finally, the fourth and so far unsubmitted study is included as Chapter 1, which therefore seems to be a pivotal study of this dissertation. While the previous (Chapter 3) study focused on song frequency, this one addresses the global variation of song complexity. The authors developed a simple but reliable song complexity metric to explore a global diversity in song complexity across thousands of passerine species. The analyses revealed that song complexity is associated with several life-history, social and environmental indices of sexual selection. This is well understood, but how to biologically interpret the following statement that "these effects disappear when spatially non-random distribution of passerine clades across assemblages or in a phylogenetic cross-species analyses were accounted for"? Although the authors demonstrate that they have included an 'easy to measure proxy for avian song complexity', they admit that their metric only represents one of several song dimensions. Are there other possible easy to get indicators for such a great analysis of avian song? The current doubts about the correct or proper choice of the song complexity indicator may be the reason why only a few studies have attempted to use automatically derived metrics to characterize song complexity over large scales (and those attempting so were criticized by the author of this dissertation, see Chapter 2).

Summary of the review: The submitted dissertation confirms that Mgr. Peter Mikula is an outstanding scientist with great potential for systematic work covering a large field of behavioral ecology. He is highly experienced in fieldwork, data analysis as well as writing scientific papers including comparative studies. It is worth noting that Peter is the first author or co-author of twelve other papers in journals with IF, not included in this dissertation. I highly recommend the submitted thesis to the defense and award its author a Ph.D. title in Zoology at the Faculty of Science, Charles University in Prague.

Praha 03.09.2020



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