

dr hab. Przemysław Chylarecki
Muzeum i Instytut Zoologii PAN
Twarda 51/55, 00-818 Warszawa
e-mail: pchylarecki@miiz.waw.pl

Review of the doctoral thesis of Marta Witkowska, MSc

entitled

"Body condition in relation to environmental factors on the breeding grounds and given stages of the annual cycle of adult Great Snipes *Gallinago media* from Eastern-European, lowland population"

The dissertation submitted for review was carried out under the supervision of Professor Włodzimierz Meissner, PhD, at the Department of Vertebrate Zoology and Ecology of the University of Gdańsk. The main part of the dissertation consists of three articles, two of which have been published in peer-reviewed journals indexed in *Web of Science*, and the third has the status of a typescript ready for submission to the journal editor:

- Witkowska M., Pinchuk P., Meissner W., Karlionova N., Marynkiewicz Z. 2022. The level of water in the river flowing through the breeding site shapes the body condition of a lekking bird—the Great Snipe *Gallinago media*. *Journal of Ornithology* 163: 385–394;
- Witkowska M., Korniluk M., Pinchuk P., Tumiel T., Karlionova N., Meissner W. The interplay between moult of flight feathers and fuelling conducted on the breeding grounds of the Great Snipe *Gallinago media* from the eastern European, lowland population;
- Witkowska M., Pinchuk P., Meissner W., Karlionova N. 2024 Body size constrains the annual apparent survival of lekking Great Snipe *Gallinago media* males of eastern, lowland population. *Journal of Ornithology* 165: 169-178.

The articles are preceded by a 34-page text containing an extended summary of the work in Polish and English, acknowledgements and a brief introduction to the published and submission-ready papers. The work also includes statements from the co-authors of the articles, detailing their contribution to the preparation of each paper. Ms Witkowska is the first and corresponding author of all the publications and there is no doubt about her leading role in the preparation of the articles as described in the statements. The publications were published in a reputable journal, ranked in the second quartile in the field of "ornithology" by *Journal Citation Reports*. Both published papers are available via Open Access.

Subject of the study and main findings

This thesis focuses on selected aspects of the ecology of the Great Snipe, a shorebird that inhabits floodplains, natural sedge and sedge-moss fens and drained post-peatland meadows of Eastern

Europe, as well as open areas above the tree line in the Scandinavian mountains. The species is known for its spectacular nocturnal lekking behaviour. In this rare mating system, males compete in small groups for access to females at communal display sites (arenas), but do not provide parental care after mating, leaving incubation and chick rearing to the females. Male displays in this species are thought to be energetically costly, with birds losing up to 5-7% of body mass per display night and rebuilding the energy stores during the day, before another night of displays. This requires easy access to rich foraging grounds that would allow males to quickly replenish energy reserves on a daily basis. As Great Snipes feed mainly on earthworms from the upper layers of the soil, the presence of favourable feeding sites close to display arenas is believed to shape the distribution of the species. In addition, Great Snipes migrate to sub-Saharan wintering grounds using non-stop flights of 4000-6000 km, requiring considerable fuelling prior to migration to sustain the energetic cost of the extreme flights.

The first paper focuses on the environmental factors that influence the variation in body mass of male Great Snipes captured at lekking sites at the peak of the breeding season. Body mass decreased as the season progressed and appeared to be dependent on water levels in the river valley. Males were heavier (i.e. had larger energy reserves) when the water level was high and when the water level showed an increasing trend in the few days before the bird was captured. A decreasing trend in body mass with season appeared to be insignificant when water levels were taken into account. However, hydrological factors explained only a small percentage (18-20%) of the examined variation in Great Snipe body mass. The authors also analysed an index of body reserves, the scaled mass index (SMI), and concluded that the SMI was highly correlated with raw mass and therefore did not appear to add any new information. However, specific analyses using SMI instead of body mass were not presented, even in the supplementary materials.

The second paper deals with the timing and process of primary moult and the build-up of energy reserves prior to the southward migration of Great Snipes of both sexes. Birds studied at two sites (Belarus and Poland) showed no temporal overlap between primary moult and pre-migratory fuelling. Males, all free from parental duties, started moulting after 20 June and stopped after replacing 5-6 (up to 7) primaries in the last days of July. They then switched to fuelling. In contrast, females that were mostly busy with incubation and possibly chick rearing, started primary moult a month later, around 20 July, and stopped it after replacing 1-2 primaries. They switched to gaining mass (energy reserves) at the same time as the males, i.e. during the last days of July and the first days of August. The fuel deposition rates of both sexes are similar and rather low at c.1% of lean body mass per day.

The third paper in the thesis presents the results of capture-mark-recapture (CMR) models applied to estimate annual survival of male Great Snipes trapped over 22 years at the Pripjat River, Belarus. The best-fitting model assumed constant male survival over the study period, with recapture probabilities varying between years. However, the second best model, which showed a broadly comparable fit to the data, suggested that male survival increased with body size. The best fitting model estimated male survival to be rather low at 0.43. Such a low survival rate for a shorebird species was explained by the "fast pace of life" syndrome, with energy-demanding lekking and long non-stop migratory flights linked to elevated metabolic rates, leading in turn to reduced longevity. However, the authors acknowledged that low survival could alternatively reflect permanent emigration of some birds not accounted for in standard CMR models, a possibility supported by a recent study showing a high rate

of lek-switching by male Great Snipes. Possible lower survival of smaller males was tentatively explained by their shorter bills resulting in lower foraging efficiency of birds searching for buried prey by probing in the mud, a result described already for other shorebird species.

Strengths of the thesis

The work is well embedded in the literature on the subject, indicating a good working knowledge of avian biology, particularly shorebird ecology. The PhD candidate has a good understanding of the benefits and costs of the deposition of energy reserves by birds, of the trade-offs in the evolution of life histories, in particular the trade-offs in energy allocation across various stages of the annual cycle of migratory birds. She is obviously familiar with the current literature in the field and up-to-date with the latest developments in bird ecology.

Throughout the thesis, the writing is clear and readable. This applies not only to the published or submission-ready articles, but also to the extended summaries of the research, which I found surprisingly useful. Both the English and Polish summaries are well structured, with clearly stated research hypotheses, concise presentation of results and clear conclusions. In the core papers, some aspects of the analyses have been moved to the (online) appendices to improve the readability of the main texts, which is clearly a good way of combining a clear narrative with the provision of additional details of the study.

The thesis is also notable for the wide range of analytical techniques used by the PhD candidate to make the most of the data available. Witkowska is well versed in data modelling and goes well beyond the simple, standard models used by many other researchers, which is one of the factors behind the interesting results she is able to obtain. Here, I acknowledge the routine use of multi-model approaches, connected with model selection and (sometimes) model averaging. I also commend the use of generalised additive models (GAMs), which allow flexibility in describing non-linear patterns in the data, as well as use of Underhill-Zucchini model to describe moult parameters. She is also to be commended for her use of capture-mark-recapture models, as implemented in the famous MARK software, a nightmare for many otherwise skilled data analysts.

Importantly, the thesis describes poorly known aspects of the biology of a bird species of European conservation concern. The Great Snipe is classified as Vulnerable in the European Union and Endangered in Poland according to IUCN criteria. Therefore, in addition to the purely scientific aspects, a better knowledge of the biology of the species resulting from the research carried out by Ms Witkowska and her team clearly contributes to the possibility of more effective conservation of this iconic bird. It is important to emphasise that the work reviewed here does indeed provide some entirely new data on the ecology of the Great Snipe on its breeding grounds. To my knowledge, this is the first paper describing in a quantitative, rigorous manner, the flight feather moult conducted by Great Snipes on the breeding grounds, prior to their migration to Africa. The only other paper dealing with moult of the species concerns birds completing their moult on wintering grounds in central Africa and published only 7 years ago.

Despite its unfavourable conservation status, our knowledge of the demography of the Great Snipe remains rather limited, with no formal analyses of the annual survival and productivity of the species published to date. Here, the paper published in 2024 by Witkowska et al. is the first to provide estimates of the apparent annual survival of the species. Although not without interpretation

problems (see next chapter), the paper paves the way for demographic modelling and population viability analyses, which are essential for effective management of populations of this endangered species. Furthermore, Witkowska is the first to quantitatively describe the process of fuel deposition rates by Great Snipes preparing to their southward migration, while on European breeding grounds. Surprisingly, despite apparently high energy demands linked to long non-stop flights, the fuelling rate turned out to be low and birds appeared to have rather low fuel loads before the migration.

Finally, the simple finding that increased spring flooding of the river valley is associated with improved body condition of male Great Snipes provides a strong argument for the conservation of undisturbed river valleys with unaltered hydrological regimes. This is urgently needed if we are to save the species from extinction across much of its eastern European breeding range.

Questions and weak points

Despite its arguably high scientific value, the thesis, like many dissertations or even published papers, is not free of shortcomings or somewhat controversial issues, which I would like to discuss. In the following, I address the several issues that, in my opinion, mark the slightly weaker aspects of the dissertation.

- The low apparent survival of male Great Snipe found in this study (0.43) remains rather puzzling. While the PhD candidate admits that low site fidelity may contribute to these results, she and her team then go on to consider these results as more reflective of true survival and develop explanations related to the increased metabolic rate of the species performing energy-demanding activities such as lekking displays and long non-stop flights. I still think that the low site fidelity of lekking Great Snipe males is a more plausible alternative. Apparently, all polygynous shorebird species (not just Great Snipe) exhibit reduced breeding site fidelity, as indexed by their low return rates (see Kwon et al. 2022), and this must bias standard CMR survival estimates ('apparent survival') downwards. To complement this reasoning, I also note that Kalas (2004) mentioned unpublished analyses of Scandinavian Great Snipe data showing much higher survival estimates ("The annual survival rate for adult birds appears to be relatively high (0.6 - 0.7 for a 1987-1996 sample from Norway (Fiske et al. manuscript)"). Finally, if the energetic cost of lekking is responsible for lower survival, it is unclear why male survival of lekking Ruff is high at 0.64-0.74 (Mendez et al. 2018).
- To support the claim that low survival is "probably a characteristic of this species" rather than a result of frequent dispersal between leks, Witkowska et al. (2024) mention that "only 13 individuals out of 314 ringed in 22 years had changed leks between seasons" in their study population. However, these 13 lek-switching birds should not be compared with 314 ringed birds, but with 73 individuals that were ever recaptured. This gives an estimated 18% of recaptured birds found to switch leks – something worth to consider.
- I note that in the model including body size as a covariate of male survival, the relative variable importance (RVI) for body size was 0.45. However, in multi-model inference, RVI is a controversial measure of actual variable importance and should be used with caution (Galipaud et al. 2014, Galipaud et al. 2017). Importantly, the lower bound for considering RVI

as an important variable is around 0.37, not 0 (Burnham 2015). Therefore, an RVI of 0.45 is not particularly suggestive of body size being actually an important predictor of survival.

- I wonder how the mean (and maximum) life expectancy was calculated in the paper reporting Great Snipe survival, as this was not described in the Methods section. This is important since the mean life expectancy of 3 years reported in the paper seems very high for a constant survival of 0.43. According to my rough calculations (see Carey & Roach 2020), the mean life expectancy of an animal with a constant annual survival of 0.43 should be around 1.2 years, although I am not an expert in life-table calculations and would be happy to learn that I am wrong.

Apart of these issues, I also noted several minor, more technical points including:

- consistent, repeated misspellings (“polygenic” in place of “polygynous”, “Saber” in place of “Seber”);
- use of R-squared as the criterion of model selection in one of the papers (although not in two others);
- providing test statistics (like Snedecor’s *F*, or Students’s *t*) without associated degrees of freedom.

I conclude this chapter by emphasizing that the above questions do not alter my view that the thesis submitted by Marta Witkowska represents a very valuable contribution to our knowledge of the biology of the Great Snipe and the ecology of shorebirds in general. Rather, I treat them mainly as points that may spark an interesting discussion and exchange of ideas, while the actual answers may require further study.

Conclusions

Between 2022 and 2024, the doctoral candidate has published two scientific articles in reputable journals indexed in the *Web of Science Core Collection*, with lead contributions to multi-authored texts, and has prepared the text of another high-quality article for publication. This fact is an unequivocal confirmation of her ability to carry out her scientific work independently, which is mentioned in the current law as a criterion for evaluating doctoral candidates. Papers presented by Ms Witkowska significantly contribute to our knowledge about avian biology and extend our understanding of shorebird ecology, which allows me to conclude that – using wording of the Act – they constitute original solution of a scientific problem. I also have no doubts that the PhD candidate has a solid knowledge of bird ecology.

The doctoral dissertation submitted by Marta Witkowska, MSc, meets the formal requirements for such dissertations set out in Article 187 of the Act of 20 July 2018 – Law on the Higher Education and Science (Journal of Laws of 2018, item 1668, as amended). I therefore request that Marta Witkowska be admitted to the next stages of the procedure to obtain a doctoral degree in the field of natural sciences, in the discipline of biological sciences.



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dr hab. Przemysław Chylarecki

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