Final Report of the project
'Sexual selection, sex-ratio and sexual dimorphism in host-parasite systems'
financed by the grant OTKA/NKFIH # 108571

The present research project was planned for a 4 years period (2013-2017), but completion was postponed to 2018. During this 5 years period, parasitologists, ornithologists, and mathematicians cooperated intensively to achieve the targets outlined in the grant proposal, at the crossing point of these rather different fields of science.

(i) We have launched a series of descriptive statistical analyzes published in *Ornis Hungarica* (a peer-reviewed local journal referenced by Scopus). These papers describe the morphometrical and phenological (migration timing) changes of small Passerines detected during a long term (> 30 years) bird ringing and morphometrical monitoring study carried out at the Ócsa Bird Ringing Station. Seven items have been published up to the present day analyzing 7 species. Two of these species are sexually dimorphic and, therefore, long-term temporal changes of sexual dimorphism can be interpreted in their cases. The Pied Flycatcher (*Ficedula hypoleuca*) exhibited an increasing sexual difference in the spring measures of wing length, in parallel with an increasing sexual difference in the spring arrival dates. Males arrive more and more earlier than females, and their wing length increasingly exceeds that of the females. This phenomenon was further analyzed in more details by Harnos et al. (2015) in the *Journal of Ornithology*. No similar trend was observed in case of the sexually dimorphic Common Blackbird (*Turdus merula*), perhaps because this species is only partially migrant in Central Europe.

Csörgő et al. 2017a. Ornis Hungarica 25 (1): 120–146.
Csörgő et al. 2017b. Ornis Hungarica 25 (1): 147–176.
Csörgő et al. 2017c. Ornis Hungarica 25 (2): 116–140.
Csörgő et al. 2018. Ornis Hungarica 26 (1): 149–170
Harnos et al. 2016a. Ornis Hungarica 24 (2): 109–126.
Harnos et al. 2016b. Ornis Hungarica 24 (2): 127–144.
Harnos et al. 2018. Ornis Hungarica 26 (1), 124–148.
Harnos et al. 2015. Journal of Ornithology 156 (2): 543–546.

(ii) Contrarily to our preliminary expectations, that might have been a bit naïve, we could not detect any meaningful relationship between the sexual dimorphism of

Passerine birds and statistical measures of their parasitic infections: no signs of an “interspecific sexual coevolution” was detected. Luckily, however, we could document the geographical and epidemiological factors influencing the sexual selection pressure exerted on parasites in another host-parasite model system. Using rough data published by former authors and applying advanced phylogenetically controlled methods, we have shown strong evidence that infection abundance (the number of parasites / hosts) strongly correlates with the sex-ratio and also with several sexually selected morphological traits in the Trichodectid lice of Pocket Gophers (Geomyidae). This constitutes one of the strongest evidence up to the present for the argument that the sexual selection pressure exerted upon parasites is strongly affected by their epidemiology. Further, we also showed evidence that parasite speciation is facilitated by sexual selection – a factor neglected by most former authors. We also determined the geographical context of these processes: intensive sexual selection and speciation occurs in a geographical center, while these processes are weak or totally absent on the geographical peripheries. We proposed a hypothesis to explain how sexual selection affects parasite virulence.

Rózsa et al. 2015. In: Morand et al. (eds.) Parasite diversity and diversification: evolutionary ecology meets phylogenetics. pp 58–76. Cambridge University Press.

(iii) In the same book, we have also published a detailed review on the factors influencing the speciation and consequent diversity of avian ectoparasites.

Rózsa 2015. Morand et al. (eds.) Parasite diversity and diversification: evolutionary ecology meets phylogenetics. pp 215–229. Cambridge University Press.

(iv) We allocated much effort to investigate the body size evolution of avian lice. First, to study a system free of the effects of sexual selection, we analyzed the evolution of female body size in parasites. Using phylogenetic generalized least squares (PGLS) methods, we have shown that most, but not all families (Ricinidae, Menoponidae, Philopteridae) and ecological guilds of avian lice (Phthiraptera: Amblycera, Ischnocera) follow the so-called Harrison’s Rule (stating that larger host tend to have larger parasites). Testing the validity of Poulin’s Increasing Variance Hypothesis (a positive relationship between host body size and the variability of parasite body size) yielded in similar results. Our work is probaly the strongest evidence for the former, and the only empirical test and evidence for the latter hypothesis. We discussed the mathematical and ecological factors that may be responsible for these patterns, and also the potential pervasiveness of these relationships among all parasites on Earth. Needless to say, the body size of parasites influences their metabolism and, consequently, their virulence as well.

Harnos et al. 2017. Evolution 71(2): 421–431.

(v) The next step was to include both male and female body sizes in the analyzes. Using the same data set and similar methods, we analyzed the evolution of sexual size dimorphism in parasites. We tested the validity of Rensch's rule, that predicts an allometric relationship between species' body size and sexual size dimorphism. We have shown that most, but not all families and ecological guilds of avian lice compile this evolutionary trend, and we have even found an example for the opposite trend. To our best knowledge, this is the second study to verify Rensch's rule for parasites. A preliminary version of this work has already been presented as a talk at an international conference and, more importantly, we submitted this manuscript to Scientific Records, got relatively supportive reviewer comments, and then resubmitted the revised manuscript (on 17. 08. 2018.) that is now waiting for a final editorial decision. As this is not accepted for publication yet, we do not list it in the project publication list.

Piross IS, Harnos A, Rózsa L 2018. Rensch's rule in avian lice: contradicting allometric trends for sexual size dimorphism. revised ms re-submitted to Scientific Records.

(vi) As the majority of us (the project participants) are mathematicians, a prominent role of the present project was to develop new biostatistical methods and also to critically test existing methods in the field of epidemiological biostatistics. Our most prominent results in this field are as follows:

a. Diversity is often measured as the mean rarity of species in a community. In behavioral sciences and parasitology, mean crowding is the size of the group to which a typical individual belongs. Focusing mostly on the mathematical aspect, we demonstrated that diversity and crowding are closely related notions. We showed that mean crowding can be transformed into diversity and vice versa. Based on this general equivalence rule, notions, relationships, and methods developed in one field can be adapted to the other one. In relation to crowding, we introduced the notion of "effective number of groups" that corresponds to the "effective number of species" used in diversity studies. We defined new aggregation indices that mirror evenness indices known from diversity theory. We also constructed aggregation profiles and orderings of populations based on aggregation indices. This was exemplified using real-life abundance data of avian parasites.

Lang et al. 2017. ECOSPHERE 8 (7): Paper e01897.

b. Prevalence of a disease is usually assessed by diagnostic tests that may produce false results. We proposed a new method to construct approximate confidence intervals for the true prevalence when sensitivity and specificity are estimated from independent samples. According to an extensive simulation study the new confidence intervals maintain the nominal level fairly well even for small sample sizes. We illustrated the advantages of the proposed method with real-life applications.

Lang et al. 2014. PREVENTIVE VETERINARY MEDICINE 113: 13–22.

c. Rudas et al. (1994) introduced the so-called mixture index of fit for quantifying the goodness of fit, aka Π*, of a model. It is the lowest proportion of 'contamination' which, if removed from the population or from the sample, makes the fit of the model perfect. The mixture index of fit has been widely used in psychometric studies. We proposed a new bias-corrected point estimate, a bootstrap test and confidence limits for Π*. These confidence limits have coverage probability much closer to the nominal level than the other methods do. We illustrated the usefulness of this method with real-life applications.

Reiczigel et al. 2017. BRITISH JOURNAL OF MATHEMATICAL & STATISTICAL PSYCHOLOGY in press.

d. The risk ratio quantifies the risk of disease in a study population relative to a reference population. Standard methods of estimation and testing assume a perfect diagnostic test having sensitivity and specificity of 100%. However, this assumption typically does not hold. We proposed procedures that control for sensitivity and specificity of the diagnostic test, given the risks are measured by proportions, as it is in cross-sectional studies or studies with fixed follow-up times. These procedures provide an exact unconditional test and confidence interval for the true risk ratio. The methods also cover the case when sensitivity and specificity differ in the two groups. The resulting test and confidence interval may be useful in epidemiological studies as well as in clinical and vaccine trials. We illustrated the method with real-life examples.

Reiczigel et al. 2017. EPIDEMIOLOGY AND INFECTION 145: (1) 187–193.

e. Finally, we gave a critical overview of former studies claiming a relationship between sample size and measures of infection intensity. Former authors claimed that, due to parasites' aggregated distribution, small samples underestimate the true population mean intensity. We showed that this claim may be false or true, depending on what is meant by 'underestimate' or, mathematically speaking, how we define 'bias'. The 'how often' and 'on average' views lead to different conclusions because sample mean abundance itself exhibits an aggregated distribution: most often it falls slightly below the true population mean, while sometimes greatly exceeds it. Since the several small negative deviations are compensated by a few greater positive ones, the average of sample means, contrary to widespread views, approximates the true population mean.

Reiczigel et al. FOLIA PARASITOLOGICA 64: Paper 025.

(vii) We further developed the technological background of our bio-statistical methodologies, including the Quantitative Parasitology software that is already used and cited across several parasite ecology labs all over the World. The new methodological results listed above are continuously being implemented into this online and free-to-access biostatistical toolbox.

http://www2.univet.hu/qpweb/qp10/index.php

(viii) We also intended to improve the methodological standards of bird ringing/banding works, both regarding the fieldwork methods and the data handling and analysis methodologies.

Csörgő et al. 2016. ORNIS HUNGARICA 24 (2): 91–108.
Harnos et al. 2015. ORNIS HUNGARICA 23 (2): 163–188.
Harnos et al. 2016. ORNIS HUNGARICA 24 (1): 172–181
Harnos et al. 2017. ORNIS HUNGARICA 25:(2) 141–156.

(ix) Finally, several circumstantial results were yielded during the course of the present project. As a necessity, the biostatistical methodologies we were working on, coming together with the equipments purchased for the aims of the present project enabled us to participate in a variety of human and animal epidemiological studies that were – admittedly – only loosely connected to the project research plan. Anyway, these are still additional benefits of our grant, just a few examples:

Fodor (…) Lang et al. 2018. ANIMAL REPRODUCTION SCIENCE 188: 114–122.
Tappe (…) Rózsa, et al. 2016. EMERGING INFECTIOUS DISEASES 22: 1333–1339.
Hardi (…) Rózsa 2017. ECOHEALTH 14:(4) 743–749.

(x) Above we summarized only the most important results of our project, but please find further publications in the attached list.