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Host-parasite relationship of birds (Aves)
and lice (Phthiraptera) – evolution,
ecology and faunistics

PhD theses

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Introduction

The host-parasite relationship is one of the most complex and intimate associations in nature. Given the astonishing diversity of parasitic animals, as well as that of their hosts, a huge variety of interactions evolved between the two partners. These interactions can be studied from several different points of view, each contributing to the general understanding of host-parasite relationships. At an ecological level, this relationship is often characterized as an arms race – emphasizing the conflicting adaptations and counter-adaptations of the partners. Nevertheless, often the present partners' ancestors have already been associated through evolutionary ages, raising the possibility to study how host and parasite lineages have affected each other's adaptation and diversification. Such studies are able to draw reliable inference only if based on a sound classical zoological background: faunistics, taxonomy, and systematics.

In this PhD thesis I present a multidisciplinary approach investigating the relationship of parasitic lice (Insecta: Phthiraptera) and their avian and mammalian hosts (Vertebrata: Aves, Mammalia). I apply both modern statistical methodologies of evolutionary comparative analysis and classical zoological methodologies such as sampling in the field for faunistical purposes. The two main chapters of the thesis indicate the two fields I was most concerned in the recent years: (i) the linkage between host and parasite diversity at a macroevolutionary level and (ii) various aspects of louse faunistics.

Louse richness is remarkably variable among host taxa. The features of the bird-louse relationship offer a unique system to study the inference of macroevolutionary and macroecological

factors shaping two closely associated lineages. In this chapter I focus on the diversity component of host-parasite relationships, using birds (and sometimes mammals) and their lice as a model system. Parasites and other pathogens have a quite specific role in the formation and maintenance of biodiversity; they not only represent themselves a considerably large proportion of biodiversity but they have a unique importance in facilitating the diversity of their hosts as well, hence contributing to the global biodiversity as a whole at a great extent.

Local faunistical surveys are essential to discover the patterns in the geographical distribution of lice, the local variability in louse-host associations and in parasite assemblages. Although faunistics is often considered to be a low-prestige field of biology nowadays, I argue that it is – and will remain to be – vital to provide basic data about the studied organisms and thus to allow further evolutionary and ecological investigations.

Aims

Here I briefly list the main questions and aims of my research.

Chapter 1 – Louse diversity and its macroevolutionary correlates

I investigated:

- whether there is a co-variation between avian cognitive/innovative capabilities and the taxonomic richness of their lice;

- whether louse diversity is reduced on brood parasitic bird clades due to the lack of vertical transmission routes (i.e. from parents to chicks) for lice;
- whether more diverse host groups harbor more diverse parasites by testing Eichler's assumption (the so-called Eichler's rule) for the first time.

Chapter 2 – Louse faunistics and conservation biology

I aimed to:

- prepare the Hungarian louse checklist by critically reviewing the literature;
- find new louse species for the Hungarian fauna by identifying the ectoparasite samples collected in the last few years by myself and my colleagues;
- test whether bird ringing procedure reduces avian louse burdens, thus causing a bias in louse infestation measures of birds sampled in bird ringing centers;
- prepare a global list of critically co-endangered and co-extinct louse species to draw attention to the conservational status and value of parasitic animals.

Results and discussion

Chapter 1 – Louse diversity and its macroevolutionary correlates

The study entitled “Clever birds are lousy: Co-variation between avian innovation and the taxonomic richness of their amblyceran lice” unveils a formerly unexpected positive correlation between the host cognitive/innovative capabilities and louse richness across avian families. Using data of 108 avian families (controlling for phylogenetic effects, host species richness within a family, body size, and research effort) I found that host cognitive/innovative capabilities and relative brain size co-vary positively with Amblyceran genera richness, but not with Ischnocerans. I propose several alternative and mutually non-exclusive hypotheses to explain this phenomenon.

The study entitled “Avian brood parasitism and ectoparasite richness – scale-dependent diversity interactions in a three-level host-parasite system” explores the effect of hosts’ brood parasitic life-style and the complex metapopulation structure of foster-generalist cuckoo species on their louse richness. Brood parasitic birds, together with their parasites and their foster birds constitute a complex three-level evolutionary system. Brood parasitic birds harbor host-specific louse species despite the complete lack of the vertical route of louse transmission, as their nestlings never get into direct physical contact with their genetic parents. I showed that host clades’ past switches to brood parasitism reduced both Amblyceran and (to a lesser extent) Ischnoceran genera richness, most probably because several louse lineages were unable to adapt to the lack of vertical transmission. On the other hand, I also

showed that the supposedly more complex and dynamic subpopulation structure of foster-generalist (i.e. utilizes several to many foster species) cuckoo species facilitates Ischnoceran species richness; hence for the first time diversity interactions across a three-level host-parasite system were recognized.

The study entitled “Evolutionary co-variation of host and parasite diversity – the first test of Eichler’s rule using parasitic lice (Insecta: Phthiraptera)” re-visits and tests with modern methodologies the more or less forgotten “Eichler’s rule”. Eichler’s original assumption that more diverse host groups harbor more diverse parasite faunae was strongly supported by my study. I found positive co-variation between the species richness of 175 avian and 147 mammalian families and the genera richness of their Amblyceran, Ischnoceran, and Anopluran lice. Host diversity proved to be the strongest predictor of parasite diversity found so far. The potential macroevolutionary and macroecological mechanisms beyond this phenomenon were also discussed.

Chapter 2 – Louse faunistics and conservation biology

I compiled a checklist of avian and mammalian lice occurring in Hungary that includes 279 louse species (and subspecies) which have been recorded since 1945. Their hosts represent 156 bird and 30 mammal species. Additionally, I also listed further 550 louse species whose occurrence may seem to be likely (as judged from their geographic and host distribution) but have not been detected yet.

I identified ectoparasite samples collected by myself and my colleagues in recent years. This study increases the number of louse species and subspecies known from Hungary to 299,

infesting 170 bird species (14 new avian host species as compared to the checklist mentioned above).

Ectoparasite sampling of wild birds is usually carried out parallel with bird ringing activities all over the World. Bird ringing stations work with the appropriate licenses issued by the relevant conservation authorities and offer excellent conditions for louse sampling as a huge number of birds belonging to several different species are caught there in standardized ways. However, the handling of host individuals during the ringing procedure may lead to ectoparasite loss. To test this idea Barn Swallows (*Hirundo rustica*) were assigned in the breeding season into two experimental groups – the birds were subjected to either a standard (recording biometry, fat and other condition scores, feather hole counts), or a reduced ringing procedure (only feather hole counts). I used feather holes (presumed traces of louse chewing) as a measure of louse loads. The birds were recaptured and holes were recounted after a month. Significantly more new holes appeared in the reduced ringing procedure group indicating that ringing procedures effectively reduces louse loads.

The global conservational status of parasitic lice was assessed by combining the known conservational status of the avian and mammalian hosts with the published information on the host-specificity of their lice. The list contains 6 co-extinct, and 40 (possibly 41) critically co-endangered louse species, and further 2 (but possibly 4) cases of conservation-induced extinction. The purpose of this parasite “red lists” is to draw attention to the endangerment of dependent taxa – such as symbionts, parasites and parasitoids – and their biological value.

Summary

Here I briefly list the main results:

Chapter 1 – Louse diversity and its macroevolutionary correlates

- a positive co-variation was detected between avian cognitive/innovative capabilities and the generic richness of Amblyceran lice;
- avian hosts' switching to brood parasitic way of life was shown to reduce the genera richness and taxonomic distinctness index of both Amblyceran and (to a lesser extent) Ischnoceran lice;
- a positive evolutionary co-variation was found between the diversity measures (species richness, genera richness, and taxonomic distinctness) of cuckoos' Ischnoceran lice and the number of their foster species; to my best knowledge, this represents the first diversity interaction ever found in a three-level host-parasite system;
- Eichler's assumption that more diverse host groups harbor more diverse parasites was revisited, tested, and evaluated by modern statistical methodologies covering the global louse fauna; this co-variation represents the strongest predictor of louse diversity recognized so far.

Chapter 2 – Louse faunistics and conservation biology

- the Hungarian louse checklist was compiled by critically reviewing the literature;
- 20 louse species were found as new to the Hungarian fauna by identifying the ectoparasite samples collected in the last few years;
- bird ringing procedure was shown to reduce avian louse burdens;
- a global list of critically co-endangered and co-extinct louse species was provided, with particular emphasis on louse species which became extinct due to conservation efforts focusing on the host.

List of publications

(in peer-reviewed journals or as book chapters between 2009-2013, related to the present thesis)

Vas Z., Fuisz T.I., Fehérvári P., Reiczigel J., Rózsa L. 2013. Avian brood parasitism and ectoparasite richness – scale-dependent diversity interactions in a three-level host-parasite system. *Evolution* **67**(4): 959-968. IF: 4.864

Rózsa L., Vas Z. 2013. A list of co-extinct and critically co-endangered species of parasitic lice (Phthiraptera) with remarkable cases of conservation-induced extinction. *Oryx*, in press. IF: 1.624

Rózsa L., Vas Z. 2013. Host correlates of diversification in avian lice. In: Morand S., Krasnov B.R., Littlewood T. (eds.) *Parasite diversity and diversification: evolutionary ecology meets phylogenetics*. Cambridge University Press, in press.

Vas Z., Csorba G., Rózsa L. 2012. Evolutionary co-variation of host and parasite diversity – the first test of Eichler's rule using parasitic lice (Insecta: Phthiraptera). *Parasitology Research* **111**: 393-401. IF: 2.852; independent citations: 2.

Vas Z., Privigyei Cs., Prohászka V.J., Csörgő T., Rózsa L. 2012. New species and host association records for the Hungarian avian louse fauna (Insecta: Phthiraptera). *Ornis Hungarica* **20**(1): 44-49.

Vas Z., Rékási J., Rózsa L. 2012. A checklist of lice of Hungary (Insecta: Phthiraptera). *Annales historico-naturales Musei nationalis hungarici* **104**: 5-109.

Vas Z., Lefebvre L., Johnson K.P., Reiczigel J., Rózsa L. 2011. Clever birds are lousy: Co-variation between avian innovation and the taxonomic richness of their amblyceran lice. *International Journal for Parasitology* **41**: 1295-1300. IF: 3.393; independent citations: 4.

Vas Z., Fuisz T.I. 2010. Ringing procedure can reduce the burden of feather lice in Barn Swallows *Hirundo rustica*. *Acta Ornithologica* **45**(2): 203-207. IF: 0.889; independent citations: 2.

Vas Z., Fuisz T.I. 2010. Rendhagyó vedlésű füstifecske (*Hirundo rustica*). *Aquila* **116-117**: 132-133.