Summary of PhD thesis

Ecological and phylogenetic comparative studies of avian lice

Imre Sándor PIROSS

Supervisors: Dr. Andrea HARNOS

Dr. Lajos RÓZSA

UNIVERSITY OF VETERINARY MEDICINE BUDAPEST

Doctoral School of Veterinary Sciences

Budapest, 2022

University of Veterinary Medicine Budapest
Doctoral School of Veterinary Sciences
Budapest, Hungary

.....

Dr. Andrea HARNOS, PhD

Associate Professor, Head of Department

Department of Biomathematics and Informatics

University of Veterinary Medicine Budapest

Supervisor

.....

Dr. Lajos RÓZSA, DSc

Scientific advisor

Institute of Evolution

Centre for Ecological Research, Budapest, Hungary

Supervisor

.....

Piross Imre Sándor

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1 Introduction

Lice (Phthiraptera) are a common ectoparasite of birds, and their relationship dates back at least 40 million years. During this period, adaptations and counter-adaptations formed an “arms race” in which bird and lice species shaped each other’s characteristics.

Avian lice spend their entire life cycle in the plumage of birds. They belong to the suborders Ischnocera and Amblycera. They primarily feed on feather material. Some groups may feed on skin debris or blood by chewing on developing feathers. Lice reproduce sexually, the females lay on average one egg a day.

Lice are typically low pathogenic parasites, causing more severe symptoms only if they are present in higher numbers on a host. The amount of feather material consumed by the lice can affect the thermoregulation of the host. They may also be vectors of microbial infections. Birds combat their lice in various ways; preening is one of the fundamental ways of this. The morphology of the beak has been partly adapted to the removal of ectoparasites. Injured birds may also be exposed to more severe lice infections depending on the nature of the injury, as it can be difficult for them to remove their parasites. Louse subpopulations are often able to overgrow in the absence of adequate defence; on the other hand, extreme infestations worsen the host's condition.

Lice are flightless insects; they can transmit by direct physical contact between their hosts. Some lice show phoretic behaviour when they attach themselves to hippoboscid flies to travel between hosts. In general, there are two transmission routes that lice can utilise: the

horizontal and the vertical transmission routes. During horizontal transmission, lice disperse among non-related individuals, for example, during mating. Vertical transmission occurs among related hosts, especially parents and offspring, or between siblings until the nestlings are still in the nest together. It is likely that lice do not disperse randomly from one host to the other, but we know little about this behaviour. Dispersion could be affected by the expected survival and reproduction chances and individual traits of the donor and recipient host.

Lice typically exhibit aggregated distributions in the natural populations of birds, similar to other parasites, i.e. a large proportion of birds are not or are only slightly infected. In contrast, a small proportion is very infected. It follows that their impact also reflects this distribution on the host population.

To examine the transmission patterns of lice, it is worth choosing a host-parasite system where they occur in large numbers, and the biology of the host species is also well known. The Common Kestrel (*Falco tinnunculus*) is widespread in the Palearctic region, with well-known breeding biology and ectoparasite fauna. Red-footed Falcons (*Falco vespertinus*) breed in the Eastern Palearctic. They show exemplary sexual dimorphism as adults while being similar as nestlings. Amur Falcons (*Falco amurensis*) have the longest migratory route among raptors. They use vast stop-over sites during their autumn migration, where hundreds of thousands of birds can gather.

Studies in the first half of the dissertation aimed to investigate how individual traits of falcons affect their louse load at different stages of their life. Our first study investigated how the sex, maturity, and clutch size of Common Kestrel nestlings affect their lice. Our second study investigated how static and dynamic traits of colonial Red-footed Falcons affect the dynamics of their louse subpopulations during the breeding period and how they affect the colonisation of new hosts by lice. Lastly, we investigated the effect of Amur Falcons' sex, age and body size on the abundance of their lice at a vast autumn migratory stop-over site.

In the second half, I investigate whether a generally observed pattern in sexual size dimorphism — Rensch’s rule — holds in different avian louse families. Rensch's rule (RR) states: in comparisons across closely related species, male body size relative to female size increases with the average size of the species.

2 The relationship of louse infestation and clutch size in the Common Kestrel (*Falco tinnunculus*)

Piross, I. S.; Saliga, R.; Solt, S.; Horváth, É.; Kotymán, L.; Harnos, A.; Rózsa, L.; Palatitz, P.; Fehérvári, P., **A tolltetű-fertőzöttség és fészekaljméret kapcsolata a vörös vércsénél (*Falco tinnunculus*)**. Magyar Állatorvosok Lapja., 745–753., 2018

Transmission of avian lice – in most cases – requires physical contact between hosts. Lice may benefit from choosing host individuals with better survival prospects and dispersal chances. Bodily contacts between parents and offsprings provide a good opportunity for host selection. Common Kestrels offer a suitable model system to study the ecological correlates of vertical transmission of lice. Our study aimed to investigate how the sex, maturity, and clutch size of Common Kestrel nestlings affect the abundance of their lice.

Fieldwork was carried out in Körös-Maros National Park Directorate (Hungary). The ectoparasites were collected from nestlings (N=54) with dust-ruffling. The effect of the host's sex, wing length and clutch size on the abundance of their lice was analysed using negative binomial mixed models.

In the case of *Colpocephalum subzerafae*, none of the investigated variables had a significant effect. Contrarily, clutch size had a significant effect on *Degeeriella rufa* abundance. In small clutches (3–4 nestlings), the mean abundance of *D. rufa* is 3.7 times higher, than in large (5–6 nestlings) clutches. We found two non-exclusive

explanations of this pattern. First, parental quality is known to affect the clutch size. If low-quality parents are also more heavily infested with lice, this could explain the higher louse load of their nestlings. Alternatively, according to the dilution hypothesis, long life-cycle ectoparasites (such as lice), which are incapable of significantly raising their subpopulation size until the chicks' fledging, disperse among the nestlings, resulting in lower per nestling louse counts in larger clutches. According to our results, both the breeding parameters and the parents' quality may affect their offsprings' ectoparasite load.

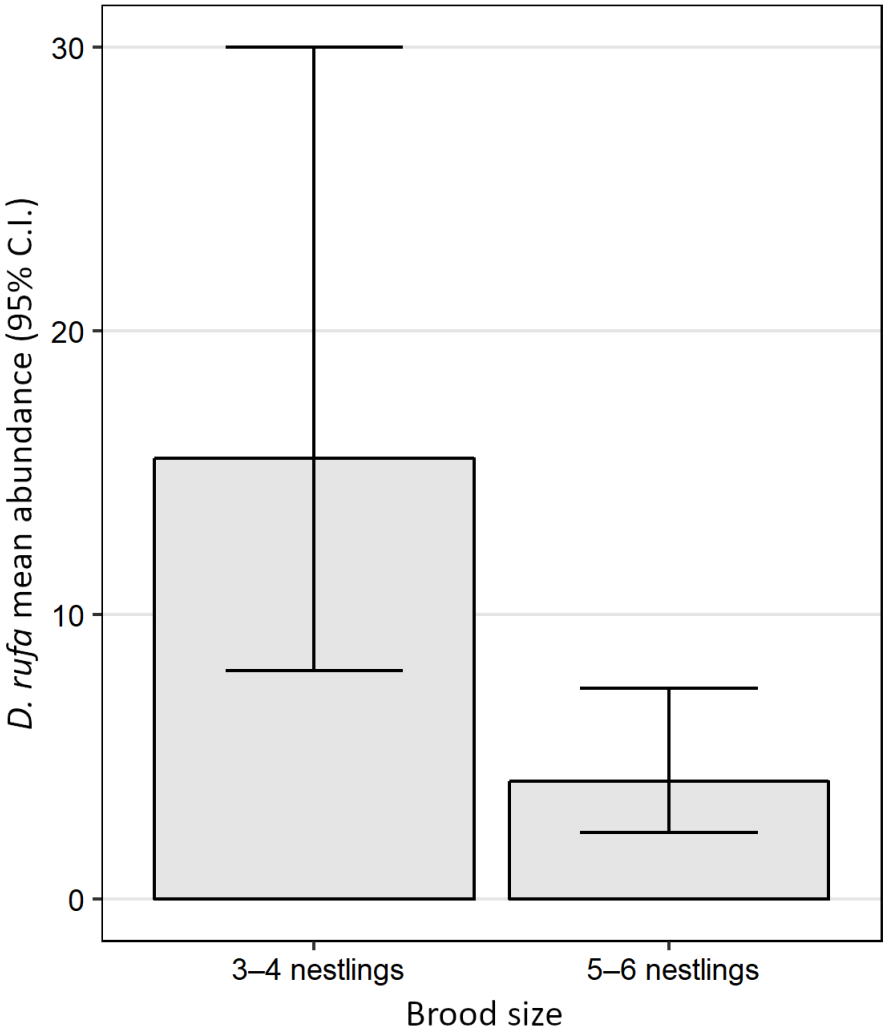

Figure 1 Mean abundance (95% confidence interval, C.I.) of Degeeriella rufa on Common Kestrel (Falco tinnunculus) nestlings in small (3-4 chicks) and large (5-6 chicks) broods.

3 Sex-dependent changes in the louse abundance of Red-footed Falcons (*Falco vespertinus)*

Based on: Piross, I. S.; Solt, S.; Horváth, É.; Kotymán, L.; Palatitz, P.; Bertók, P.; Szabó, K.; Vili, N.; Vas, Z.; Rózsa, L.; Harnos, A.; Fehérvári, P., **Sex-dependent changes in the louse abundance of red-footed falcons (*Falco vespertinus*).** Parasitology Research., 119, 1327–1335., 2020

Permanent ectoparasites live in stable environments; thus, their population dynamics are primarily adapted to host life cycle changes. We aimed to investigate how static and dynamic traits of colonial Red-footed Falcons interplay with the dynamics of their louse subpopulations during the breeding period and how they affect the colonisation of new hosts by lice.

We sampled Red-footed Falcon (*Falco vespertinus*) nestlings in two and adults in one breeding season. The mean abundance of *Colpocephalum subzerafae* and *Degeeriella rufa* lice on the nestlings was modelled using clutch size and host sex in interaction with wing length. For the adults, we used wing length and the number of days after laying the first egg, both in interaction with sex.

D. rufa abundances increased with the nestlings' wing length. In one year, this trend was steeper on females. In adult birds, both louse species exhibited higher abundances on females at the beginning, but it decreased subsequently through the breeding season. Contrarily, abundances were constantly low on adult males.

Apparently, *D. rufa* postpones transmission until nestlings develop juvenile plumage and choose the more feathered individual among siblings. The sexual difference in the observed abundance could either be caused by the different plumage or the females' preference for less parasitized males. Moreover, females likely have more time to preen during the incubation period, lowering their louse burdens. Thus sex-biased infestation levels probably arise due to parasite preferences in the nestlings and host behavioural processes in the adult falcons.

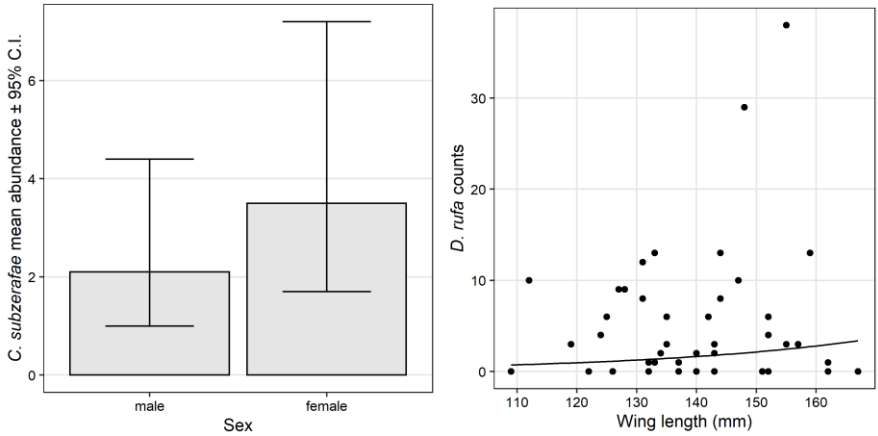

Figure 2 Results of the GLMMs modelling the mean abundance of the louse species on the Red-footed Falcon (Falco vespertinus) nestlings in 2012. In the case of the Colpocephalum subzerafae, a non-significant difference can be seen between the two sexes. In the case of Degeeriella rufa, the mean abundance increases with the wing length of the nestlings.

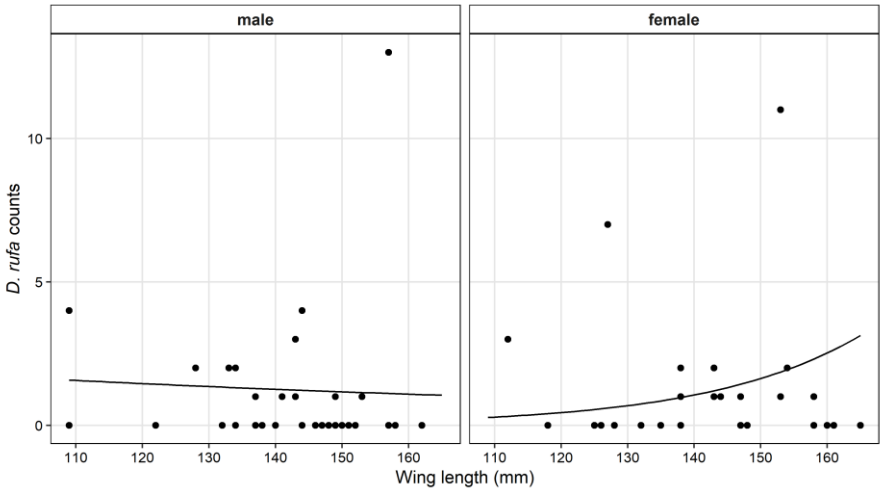

Figure 3 Results of the GLMM modelling the mean abundance of Degeeriella rufa on the Red-footed Falcon (Falco vespertinus) nestlings in 2014. There is an interaction between sex and wing length. The mean abundance increases with wing length in the case of the females.

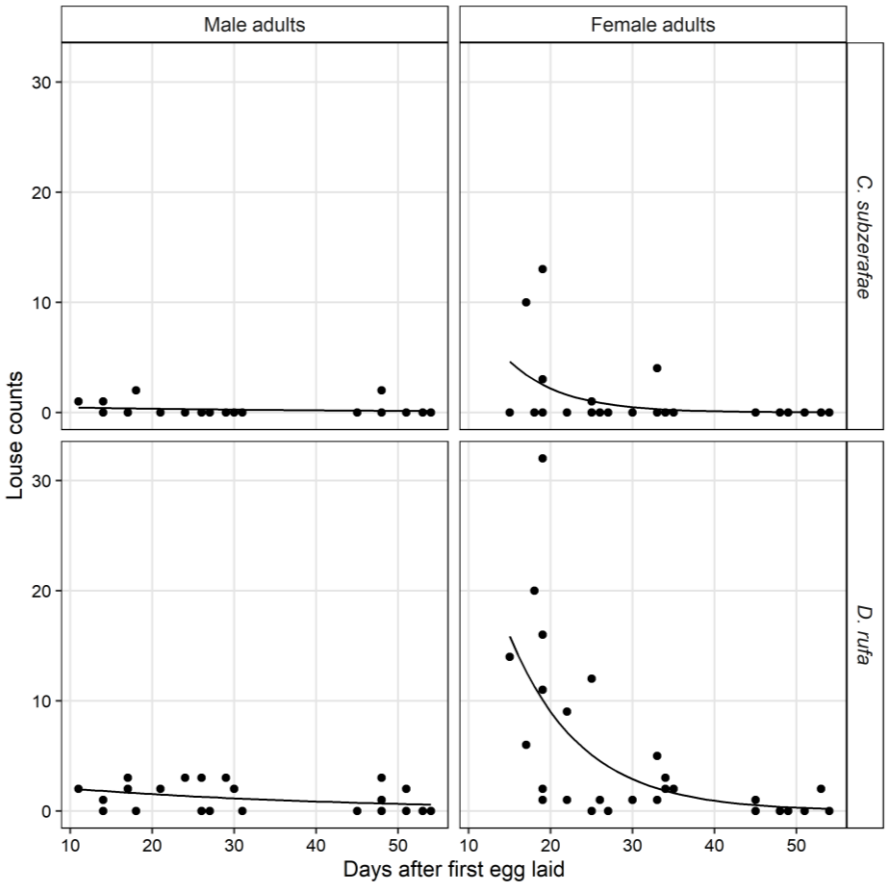

Figure 4 Results of the GLMMs modelling the mean abundance of the louse species on the adult Red-footed Falcons (Falco vespertinus) in 2014. There is an interaction between sex and the number of days after the first egg was laid in both louse species. The mean abundance of lice decreases with the number of days passed on female birds, while males maintain a low abundance level.

4 Sex interacts with age-dependent change in the abundance of lice infesting Amur Falcons (*Falco amurensis*)

Piross, I. S.; Siliwal, M.; Kumar, R. S.; Palatitz, P.; Solt, S.; Borbáth, P.; Vili, N.; Magonyi, N.; Vas, Z.; Rózsa, L.; Harnos, A.; Fehérvári, P., **Sex interacts with age-dependent change in the abundance of lice infesting Amur Falcons (*Falco amurensis*)**. Parasitology Research, 119, 2579–2585., 2020

Sex-biased and age-biased parasite infections are common in nature, including ectoparasites-vertebrate host systems. We investigated the effect of Amur Falcons' sex, age and body size on the abundance of their lice at a migratory stop-over site, where the falcons' habitat use, and behaviour are more homogeneous across sex and age categories than during the breeding season.

We sampled Amur Falcons in Nagaland, India, at major roosting sites in 2016. We applied generalised linear models (with negative binomial distribution and log-link) to model the abundance of their two most numerous lice (*Colpocephalum subzerafae* and *Degeeriella rufa*) using the host age category (juvenile or adult) and wing length, both in interaction with sex, as explanatory variables.

The abundance of *C. subzerafae* was only affected by host age, being nearly four times higher on juveniles than on adults. Juveniles were also more infested with *D. rufa* than adults. Additionally, the abundance of the latter species was lower on adult male Falcons as compared to adult females.

A juvenile bias in ectoparasite infestations is common in nature, probably due to juveniles being immunologically naïve, more resource-limited, and may be inexperienced in body maintenance behaviours like preening and grooming. On the other hand, female-biased infestations are much rarer than male-biased infestations. We briefly discuss the possible causes of female-biased infestations on Amur Falcons reported here, and in the closely related Red-footed Falcon and Lesser Kestrel as reported in the literature.

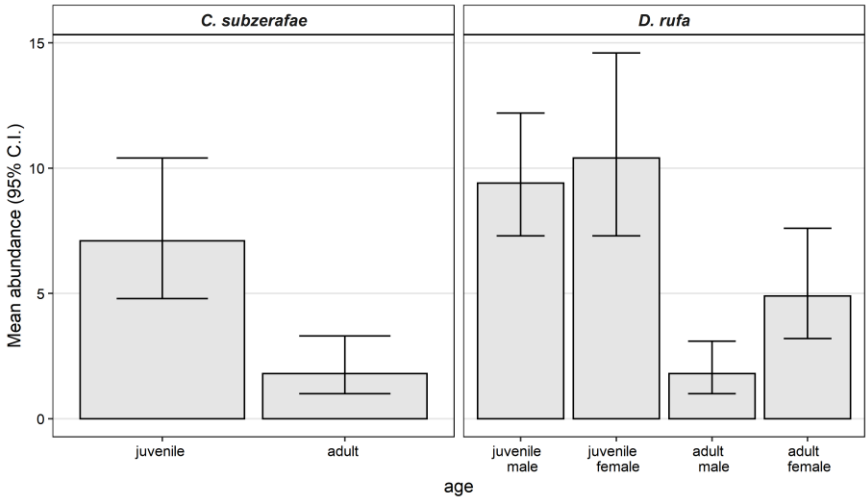

Figure 5 Results of the GLMs modelling the mean abundance of the louse species on the Amur Falcons (Falco amurensis). The mean abundance of Colpocephalum subzerafae is higher on juveniles than on adults. In the case of Degeeriella rufa we found interaction between the sex and the age of the birds. The mean abundance of D. rufa is similarly high among juveniles for both sexes, while it is higher for adult females than adult males.

5 Rensch’s rule in avian lice: contradictory allometric trends for sexual size dimorphism

Piross, I. S.; Harnos, A.; Rózsa, L., **Rensch’s rule in avian lice: contradictory allometric trends for sexual size dimorphism**. Scientific Reports., 9, 7908., 2019

Rensch's rule (RR) postulates that in comparisons across closely related species, male body size relative to female size increases with the average size of the species. This holds true in several vertebrate and also in certain free-living invertebrate taxa.

We studied the validity of RR in avian lice in three families (Philopteridae, Menoponidae, and Ricinidae). We used published data on the body length of 989 louse species, subspecies, or distinct intraspecific lineages. We applied phylogenetic reduced major axis regression to analyse the body size of females vs males while accounting for phylogenetic non-independence.

Our results indicate that philopterid and menoponid lice follow RR, while ricinids exhibit the opposite pattern. In the case of philopterids and menoponids, we argue that larger-bodied bird species tend to host lice that are both larger in size and more abundant. Thus, sexual selection acting on males makes them relatively larger, and this is stronger than fecundity selection acting on females. Ricinids exhibit converse RR, likely because fecundity selection is stronger in their case. Body size is under strong selective pressure to avoid preening while the sexes' relative size should facilitate mating. However, it seems on a grander scale there are other selection forces at play as

well. These are most likely not related to ectoparasitism since RR and CRR occur in many different animal taxa.

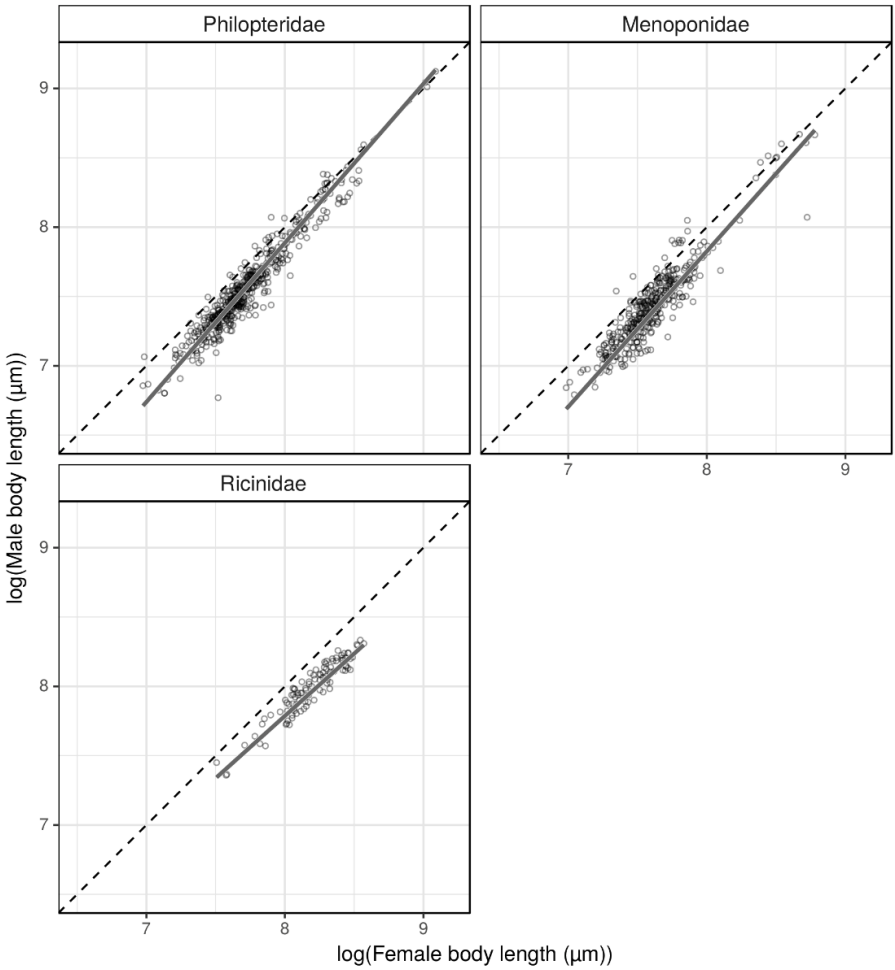

Figure 6 Allometric relationships of the louse families. Allometric relationship between log-transformed male and female body lengths (µm) with isometric slopes (dashed lines) and fitted phylogenetic reduced major axis regression lines (solid lines) by louse families.

6 Novel scientific results

First, we conducted observational studies on small falcon species to analyse the relationship between their individual traits and their lice's abundance.

- We found that *Degeeriella rufa,* on average, was more abundant on kestrel nestlings (*Falco tinnunculus*) in smaller broods.
- We found that *Degeeriella rufa, on average,* was more abundant on larger red-footed falcon (*Falco vespertinus*) nestlings. This may be in interaction with sex, where only female nestlings show this pattern.
- We found that the average abundance of *Degeeriella rufa* and *Colpocephalum subzerafae* decreased over the breeding period on adult female Red-footed falcons. The abundance on males remained constantly low.
- We found that *Degeeriella rufa* and *Colpocephalum subzerafae*, on average, was more abundant on first calendar year Amur falcons (*Falco amurensis)* than on adults during their autumn roosting period.
- *Degeeriella rufa*, on average, was also more abundant on adult females than adult males in the same autumn roosting period.

Second, we performed a phylogenetic comparative study on the sexual size dimorphism of avian lice.

- We found that the relative male size — compared to females — increases with the average size of the species in the Philopteridae and Menoponidae families, meaning they follow Rensch's rule.
- We also found that the relative male size — compared to females — decreases with the average size of the species

in the Ricinidae family, meaning they follow the converse of Rensch’s rule.

7 Publications peer-reviewed journals related to the thesis

Piross, I. S.; Saliga, R.; Solt, S.; Horváth, É.; Kotymán, L.; Harnos, A.; Rózsa, L.; Palatitz, P.; Fehérvári, P., **A tolltetű-fertőzöttség és fészekaljméret kapcsolata a vörös vércsénél (Falco tinnunculus): The relationship of louse infestation and clutch size in the Common Kestrel *(Falco tinnunculus)*.** *Magyar Állatorvosok Lapja*., 745–753., 2018

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